A Beginner’s Guide to Animal Behavior

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Chapter One

The Biology of Behavior

Imagine that you are sitting at your kitchen table. It is a beautiful summer morning and the screen door slaps shut after the dog has pushed it open with her nose to go outside. As you take your first sip of coffee, a housefly that entered when the dog exited suddenly claims your attention. Like a tiny vulture, the fly circles above the table, slowly descending, until she lands close to the sugar bowl. The fly walks toward the bowl, and stops where a few grains of sugar spilled when you lifted your spoon from the bowl two minutes earlier. The fly inflates her proboscis and begins to dab at the sugar. As you watch this, you probably begin to feel a mild sense of outrage, not because the fly is stealing sugar, but because the fly's moist, spongy proboscis, now dabbing at your table, was recently outside, probably dabbing at dog feces or at rotten chicken in the garbage can. You wave your free hand at the fly and she jumps into the air and hovers nearby before quickly landing at the sugar. You bring your hand rapidly down, attempting to crush the fly, but she is too quick for you. You put your coffee cup down, rise, and reach for the fly swatter, a tool that humans with their big brains have invented to crush flies. The flyswatter effectively doubles the length of your forearm and so doubles the speed of your strike. As you swing the flyswatter at the fly, that has resumed dabbing at the sugar, you also flex your wrist, further increasing speed. The fly sees the rapidly approaching head of the flyswatter. She jumps and begins to fly, but the broad head of your simple tool stops her flight and crushes her with enormous force into the table top. Her internal organs, including her brain, are crushed beyond repair. A tiny marvel of miniaturized circuitry and engineering lies mangled on your table. In your own brain, the circuits that would trigger shame or remorse do not light up. You brush the twitching carcass to the floor and step toward the door, where the dog is scratching to be let in.

The first thing that I want to say about this ordinary moment in life is to note how extraordinary the performances of you, the fly, and the dog were. The three of you used sensors that are tuned to radiation in certain parts of the electromagnetic spectrum, as well as sensors (in the dog and the fly) tuned to detect certain chemicals in the environment, to extract useful information about your environments. Your brains then issued precise sets of commands to muscles that pulled in a complex way on your skeletons, causing your bodies or parts of your bodies to move through space in a smooth, goal directed way. The performance of the three of you was far more impressive than anything that modern human technology can create. Robots that act like Commander Data, in the continuing voyages of the Starship Enterprise, are still entirely in the realm of science fiction, as are robots that could emulate a dog or a housefly. Unlike the Roomba, with a behavioral repertoire that consists of rolling on a flat surface and sucking dust, real animals move through a complex three-dimensional environment, detect and analyze information in multiple domains, acquire their own energy, repair themselves, and reproduce!

A neurobiologist who studies the cerebellum, a part of the brain that controls movements, once remarked that, “Moving the skeleton is an engineer’s nightmare.” Yet animals, such as you, the dog, and the fly, make very smooth, precisely timed and impeccably directed movements. The way that each of you produces movements is essentially identical. You, the dog, and the fly have sense organs, which transduce environmental energy or materials into patterns of nerve signals. Each of you uses sense organs called eyes to transduce light, energy from a narrow band of the electromagnetic spectrum. Each of you has sensors that bind to certain chemicals in the environment and transduce this event into patterns of nerve signals. For you and the dog, these chemical sensors are in the nose; in the fly, the sensors are on many parts of the outer body, including the feet – that’s how the fly knew to stop and extend her proboscis when she walked into that sweet spot on your table. Animals have a variety of sense organs, each tuned to a different source of environmental energy or materials, and across animal species, the same class of sensors may be tuned differently. The dog cannot see all the colors that you do, but the fly can. The fly can see the pattern of polarized light in the sky, but you and the dog cannot. The dog and the fly have chemical sensitivity that is greater than yours. Given the sense organs that it possesses, as well as the sensitivity and tuning characteristics of those sense organs, each animal species has its own perceptual world. I will return to this point in the next chapter.

Each animal species also has a rich variety of internal sensors, which report information about the current functioning of the body. You and the dog have receptors that report on blood temperature, sugar level, and acidity, the amount that each muscle is stretched, the likelihood that damage is occurring, mechanical pressure at most parts of the skin, how much the muscular walls of each blood vessel are contracted, the position of your head and of your eyes, to list a few examples. In summary the internal sensors report on the biochemical and mechanical integrity of the body, as well as on body part position.

Now, where do all of these reports, from the sense organs and from the internal sensors, go? They go, in you, the dog, and the fly, to the brain. A brain is an integration and command center. A brain receives reports from the sense organs and the internal sensors, integrates the information to create priorities and then, based on the priority list, issues commands. These commands are of two sorts. First, there are commands to the organs – to the heart, lungs, gut, blood vessels, and endocrine glands. These commands are concerned with the essential task of keeping the body running. Howver, as we saw in our summer tableau, an animal must do more than simply rest, plant-like, in a steady state; it must also move through its environment. This is where the second sort of commands comes in. These are the commands to the muscles that pull on the skeleton and produce movements. We call these movements behavior.

Muscle is tissue that is specialized to do one thing: to shorten on command. Muscle tissue is evolutionarily ancient and in all animals, muscle operates the same way. A command from the brain, traveling along what we call a motor nerve, reaches a muscle. The muscle, in response to the commands, uses stored energy to contract: to become shorter. The exact molecular mechanism by which shortening occurs is complicated and is now almost completely described and understood. Muscle shortening produces movement in most animals because each muscle is attached to a rigid skeleton (internal in you and in the dog, external in the fly) at two points that are on opposite sides of a flexible skeletal joint. When the muscle shortens, one part of the skeleton moves with respect to the other. For example, your biceps brachii muscle has two close points (biceps = 2 heads) of attachment (what we call the origin, or relatively fixed location) on your shoulder blade and its other point of attachment (what we call the insertion, or moveable location) on the arm bone below your elbow. When the biceps contracts, the forearm moves toward the shoulder. Essentially all animal movement is produced this way – by muscles pulling at the skeleton. A cheetah sprinting in pursuit of a gazelle, a bumblebee flying over a meadow to land on a flower, a great blue heron stabbing at a fish, a bird of paradise hopping electrically around his display area to attract a female, bullfrogs calling, crickets chirping, Hillary Hahn playing the Bach D minor Ciaccona, a baby smiling – all are the outcomes of patterns of muscle contraction.

I mentioned that animal brains are integration and command centers that receive internal and external sensory information and then issue commands. The commands to skeletal muscles cause the movements that we call behavior. How does the brain make a decision about which commands to issue? Although biologists do not understand very much about brain decision making, they are quite certain about the general design features that they expect. In other words, we can predict the general decision making rules that brains should use. In animal behavior, we make a single, quite powerful assumption about the way that brains are organized. We assume that brains are organized so that from moment to moment, individual animals act as if they are asking themselves the following question: "What should I be doing at this moment to maximize my lifetime reproductive success?" In the past 20 years we have learned is that animals in nature really do act this way and that they give the impression of being aware of the complex contingencies that go into such a calculation.

To accept this conclusion, must we accept that all animals consciously make decisions and are capable of the mathematics or at least the complex reasoning required? You might be inclined to accept this notion for yourself and perhaps for the dog, but you would probably reject it for the fly. You would be correct about the fly and incorrect about the dog and about yourself.

CLEVER HANS

In the late nineteenth century, Wilhelm von Osten startled the public and professional psychologists by showing that his Arabian stallion, Hans, could perform arithmetic calculations, including addition, subtraction, multiplication, and division, using integers or fractions, take simple square roots, tell time, read, and spell. Von Osten put questions to Hans orally or using a blackboard. Hans pawed with a forefoot repeatedly to indicate the correct answer. Von Osten: "Hans, what is the answer to 10 divided by 2"? Hans paws five times. Von Osten was convinced that animals have mental capacities that are essentially equivalent to those of humans, and he toured with Hans to prove this point. A panel of experts convened and its conclusion was that no trickery was involved. Hans gave correct answers even when von Osten was not present, and proved to have formidable computational powers. The conclusion that a horse could do math seemed inescapable.

Then a student, Oskar Pfungst, made a critical observation. If Hans was performing outside in the evening, his error rate increased as the sky darkened. Pfungst also used visual barriers and blinders and showed that Hans' ability was dependent upon his ability to see his questioner. In a startlingly clever set of experiments, Pfungst arranged for questions to be put to Hans when neither the questioner, nor anyone that Hans could see, knew the correct answer to the question. In these trials, Hans suddenly could not do the math. Pfungst concluded that Hans must be responding to unconscious cueing by humans. Pfungst noted that when Hans, pawing with a forefoot, approached the correct answer, von Osten and others performed very slight, almost unnoticeable movements, such as raising or lowering the head by a fraction of an inch, or tiny changes in facial expression. At the moment that Hans reached the correct answer, the release of anticipation in the human would create a tiny twitch or jerk. So what Hans had really learned was not math, but that to get von Osten's training rewards, to start pawing in response to the postural cues that accompanied a question, to slow pawing when subtle postural changes indicated that he was near the answer, and to stop pawing when he observed the little movement that indicated release of tension in the human. Pfungst discovered the phenomenon of unintentional cueing, which modern experimental psychologists call the Clever Hans Effect, and assiduously avoid in their experimental designs.

There are several lessons embodied in the story of Clever Hans. One is that animals may be sensitive to events that we are not aware of. Another is that experiments need to be designed to avoid unintentional cueing. For example, when Sue Savage-Rumbaugh was investigating the language capacity of apes, Kanzi the Bonobo wore headphones. An experimenter in another room spoke to Kanzi over a microphone. A dozen or so photographs were on the table in front of Kanzi, who was taught to pick up the photo that represented the word that he had heard through the headphones. Another experimenter who was in the room with Kanzi then reported his choice over a microphone to the room where the questioner sat. So Kanzi could not see the questioner, and the person in the room with him did not know the answer to the question. A third lesson that can be taken from the story of Clever Hans is the point that I want to make in the context of this chapter: is it reasonable to believe that animals can act *as if* they have complex contingencies in mind, and have conscious goals? Clever Hans shows us that the assumption is completely reasonable. Hans acted as if he could perform arithmetic when the mechanism underlying his behavior was much simpler than math ability. A housefly can act as if she is constantly thinking about what she should be doing from moment to moment to maximize the lifetime number of her eggs that hatch when her brain is far too small to produce anything like conscious thought.

ETHOGRAMS

In 1973, the Nobel Prize in Medicine went to three European biologists, Konrad Lorenz, Niko Tinbergen, and Karl von Frisch. These men received the prize for the significant insights and discoveries that each had contributed, but also because they were leaders in a new field of Biology called Ethology. The Nobel Prize affirmed that Ethology represented a significant intellectual shifting; one might even say a thought revolution, in Biology. What was the nature of the shift? It was that the behavior of animals was a proper subject for biological study. In other words, just as one may study a species' skeleton, or organs, or muscles, so one may study a species' behavior.

All individual animals have a genotype, a unique combination of genes inherited from a mother and a father. Some of these genes direct the assembly of the individual from a fertilized egg, and cause the body to be built in a species-specific way. During the assembly process, different sorts of environmental influences modulate the action of genes. The result is a phenotype, a particular body form that is species-specific, but with some amount of variation among individuals. For example, the phenotype of any human is more similar to the phenotypes of other humans than it is to the phenotype of any other species, including that of our very close relatives, the chimpanzees. However, within humans, there is obvious phenotypic variation. Some humans have light skin and some have dark skin. Human adult height ranges from under 5 feet to over 7 feet. And so on. The intellectual contribution of Ethology was to recognize that behavior is just another aspect of phenotype, like skin color or stature. So, just as we can study the inheritance, development, evolutionary history, and survival value of, say, some part of the skeleton, so we can study the inheritance, development, evolutionary history, and survival value of behavior.

I wrote that the phenotype of each species is unique – each member of a species has a phenotype that it shares with other members of its species. For physical aspects of phenotype, such a bones, this fact is obvious. The human femur, or thighbone, for example, has a length, shape, and protuberances that identify it as uniquely human. Can we prove the same assumption for behavior? Does behavior have aspects, such as length, shape, and protuberances that can be measured? The answer is yes, and the ethologists provided the proof.

The proof came from a deceptively simple technique – watching animals – but watching animals for long periods of time with patience, unwavering focus, and a willingness to suspend interpretation. When you watch an individual animal of any species for an hour or two (behavior is a unique aspect of phenotype in that it is expressed over time, so one must be willing to devote time to see the phenotype), you begin to see that behavior is not continuous improvisation. There are repeating units of behavior.

The ethologists referred to these repeating units as Fixed Action Patterns. The designation “fixed” meant that the movement in question had the same form every time that it was performed. What do I mean by “the same form?” I mean two things. First, “same form” means that if we describe the movement using technology such as slow motion film or video analysis, we see that the duration of the action, the sequence of flexion or extension of joints, and the degree to which each joint is flexed or extended, is essentially the same each time that the action is performed. Second, and more fundamentally, “same form” means that the sequence and duration of individual muscle contractions that create the joint flexion or extension is the same each time. We can discover whether the muscles that create the movement are made active in the same pattern each time by using a fundamental physiological technique called electromyography or EMG. When a muscle contracts, a weak electrical event sweeps across its surface. By attaching electrodes to the muscle, we can monitor when it is contracting and how forcefully it is contracting.

Any motion that you or any other animal performs is the result of a closely coordinated sequence of contractions of individual muscles. For example, think about what you were doing just before you first noticed the fly descending to your table. You raised the coffee cup to your lips, tilted it, and introduced some coffee into your mouth. Then, quite unconsciously, you moved the liquid in your mouth to the back of your throat, across the top of your windpipe, and into the top of your esophagus – you swallowed. That motion, swallowing, involved a precisely timed sequence of contraction of about a dozen separate muscles in your throat. Had one of the muscles started to contract one-tenth of a second too early or too late, the smooth movement of coffee into your esophagus would not have occurred.

Consider another famous Fixed Action Pattern made famous by ethologists – egg rolling. No, this is not the spring activity on the White House lawn. The motor pattern exists in a number of waterfowl. Picture a goose parent, incubating eggs on a nest. Now we place an egg or an egg-shaped object in front of the nest. The parent, which may have been looking to the side, suddenly turns to stare directly at the egg. For the moment, the egg claims all the parent's attention. After a few seconds, in which the bird's brain processes the sensory information and reaches the conclusion that the object really is an egg, the parent stretches its neck forward, places its bill over the far side of the egg, and tucks the bill toward its chest, drawing the egg into the nest. The action obviously evolved because parents that retrieved wayward eggs back into the nest left more surviving offspring then parents that did not retrieve. A variety of objects will suffice to initiate this motor sequence in an incubating parent, and once initiated, the action runs, machinelike, to conclusion. One can even reach in and remove the egg – the parent will continue with the tucking motion as if the egg is still present.

The extraordinary feat of the ethologists was that they did not reach their conclusion about repeating units of behavior with slow motion film analysis or EMG. They simply watched animals with enough attention to perceive this truth. They also realized that one could compile a catalog of all the action patterns in the repertoire of a species. The term that emerged for such a catalog was ethogram. An ethogram for a species comprises a short descriptive phrase to denote each action, accompanied by a succinct description of the movement, for all movements performed by the species.

As ethologists continued to construct and to refine ethograms, they realized that not all motor patterns were as lengthy as egg rolling. However, the longer duration motor patterns were an entry point that allowed ethologists to appreciate that behavior is composed of fixed, repeating units. This fundamental insight has held up for over half a century, and has directed the investigations of several generations of neurobiologists. Today, there is some debate over the nature of the indivisible units, but little debate over the existence of such units.

Constructing an ethogram for a species is an interesting experience. The level of concentrated attention that is required to discriminate between individual motor acts is quite different from our usual mode of looking at things. Then, when you acquire the intensity of focus that is needed to see the motor patterns of a species that you watch, your perception is forever altered – it is like learning to read, and it is fun.

Another fundamental insight emerged from the construction of carefully done ethograms in an increasing number of species. This was that patterns of similarity and difference in ethograms mirror evolutionary relatedness. If two species are closely related, meaning that they have recently diverged from a common ancestor, their ethograms are quite similar. That is, the lists of motor patterns of the two species will be very similar and the individual motor patterns will be similar in form. In contrast, if two species are not closely related, meaning that considerable time has passed since divergence from the last common ancestor, their ethograms are dissimilar. For example, humans and chimpanzees are closely related and they have quite similar ethograms. Both species laugh. Both beg by holding out a hand, palm up. In zoos, chimpanzee exhibits hold human attention far longer than any other any other exhibits because we humans are able to intuitively understand much of chimpanzee behavior. In contrast, humans are quite distantly related to lions, have a much smaller shared ethogram with lions, and have a much weaker intuitive understanding of lion behavior.

The fact that patterns of similarity and difference in ethograms match patterns of phylogeny (evolutionary relatedness) was powerful evidence that the ethologists were correct in their assertion that behavior is an aspect of phenotype. It was already widely known that patterns of anatomical similarity and difference matched phylogeny. Darwin and earlier biologists had shown this. Now the ethologists had figured out a way to describe the “anatomy” of behavior and had found the same pattern. Thus, motor patterns are gained, lost, and modified within any evolutionary lineage of animals.

BEYOND ETHOGRAMS - TINBERGEN'S FOUR QUESTIONS

In a now famous 1963 paper[1], Niko Tinbergen, who would share the Nobel Prize 10 years later, outlined his thoughts on how ethologists should set research goals after ethograms. Tinbergen had two main goals in his essay. First, he wanted to give full credit to Konrad Lorenz (another of the 1973 Nobel Laureates) who he considered to be the father of modern Ethology. Lorenz, more than anyone else, should be recognized as the principal champion of the view that behavioral traits were biological traits. Second, Tinbergen argued that to fully understand any motor pattern, one needed to amass knowledge about it in four domains. We now refer to these as Tinbergen's four questions. The domains, in the order listed by Tinbergen, are as follows.

Causation

This domain embodies two sorts of information. First, what external stimuli are necessary and sufficient to elicit the motor pattern? For an incubating goose, we know that the stimulus needed to elicit egg rolling must be essentially egg shaped, and we know that a larger than normal egg-like object is even more effective than a true egg. By experimentally altering the nature of the "egg" that we present to the

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[1] Tinbergen, N. 1963. "On aims and methods of ethology." *Zeitschrift für Tierpsychologie* 20:410-433.

goose, we can discover the precise aspects of a stimulus (the ethologists used the term Sign Stimulus) that turn on (the ethologists used the term "release") the egg rolling motor pattern. Second, what is the nature of the "wiring diagram," the brain architecture, that identifies the stimulus, makes the decision to turn on egg rolling, and issues the specific commands to muscles? For all but the simplest behavioral acts, we have only vague answers to this set of questions. Even for a housefly, the switching mechanisms that direct movement from one moment to the next turn out to be hideously complicated.

Survival Value

Next, Tinbergen turned to a domain that was controversial and little studied at the time. The domain concerns how a behavioral act contributes to the survival, and ultimately to the reproductive success of the animal that performs the act. In other words, this domain is about the organizing principle of animal brains that I mentioned earlier. Biologists now expect that animal brains are organized so that from moment to moment, each individual animal acts as if it is constantly asking itself the question: "what should I be doing at this moment to maximize my lifetime reproductive success?" However, when Tinbergen wrote his paper, many biologists thought that study of the function of behavior (how behavior contributes to survival and reproductive success) was not possible. Tinbergen pointed out that patient observation of animals in nature leads to hypotheses about function.

> “First, as one becomes better acquainted with a species, one notices more and more aspects with a possible survival value. It took me ten years of observation to realize that the removal of the empty eggshell after hatching, which I had known all along the Black-headed Gulls to do, might have a definite function…” (Tinbergen 1963 p. 422.)

Further, Tinbergen showed, in pioneering studies, that experimental tests of these hypotheses could be conducted in nature. He tested the hypothesis that eggshell removal by gull parents contributed to the survival of young by scattering gull eggs in an area where bird predators of eggs hunted. He placed empty eggshells near some of the eggs, and showed that predators found these more quickly than the eggs with no eggshells nearby. Field tests of hypotheses about the function of behavior are now very common and they constitute the majority of research now done in animal behavior today. These researchers are standing on the shoulders of Tinbergen, who in his day met the arguments of many vociferous skeptics who claimed that study of the function of behavior was impossible.

Ontogeny

Ontogeny means development. Here, Tinbergen applied his characteristic lucidity to a vexatious issue – the nature-nurture debate. At the time, this was essentially a European-American debate. The European ethologists, with a tradition of observing animals in nature, contended that many behavioral acts, such as egg rolling, were instinctive (their term was “innate”). The acts appeared in perfect form the first time that the animal perceived the appropriate stimulus. American psychologists, in contrast, had a rich tradition of experimentation and careful consideration of experimental design, using a few domestic species (mainly Norway rats, house mice, and pigeons) in controlled laboratory settings. The Americans contended that many, if not all behavioral acts, when studied carefully, could be shown to be influenced by learning. Thus, a lively and contentious transatlantic debate arose on whether motor patterns were instinctive (innate) or learned. This was the nature-nurture debate.

Tinbergen pointed out that the debate as framed was not useful. He noted that when we label an act as either innate or learned, we are making a statement about the role of experience in the development of the act. Labeling an act as instinctive implies that the act develops with no experience of any sort required. But, Tinbergen argued, proving that no experience is required means that we must experimentally prove that one type of experience after another is not needed: ultimately, we are faced with an almost endless number of negative proofs. A complimentary difficulty arises when we want to claim that an act is learned. Experimentally showing that learning is involved in the development of an act does not prove that all aspects of the act require experience – we are now faced with another endless list of positive proofs. Tinbergen argued that, rather than labeling an act as instinctive or learned, and then arguing about it, we can more profitably just study the development of the act, recognizing that most acts will develop through an interesting blend of prewired (innate) and experience-dependent (learned) mechanisms. I will give some specific examples of how the blend work in Chapter 5.

Although Tinbergen and many others since then pointed out that the debate was essentially vapid, nature-nurture is alive and well today: it arises, Phoenix-like, in the scientific literature and it is promulgated vigorously by the popular media, who are well practiced in the preservation of simplistic controversies as a way to sell stories.

Evolution

Tinbergen's fourth and final domain was about evolutionary change in behavior. What is the pattern of evolutionary change in behavior, and by what process does such change come about? Ethologists had already shown that the more closely related two species were, the more similar their ethograms were. The differences in ethograms among species must be the result of evolutionary change. Tinbergen pointed out that a careful comparison of ethograms across an array of related species would allow us to describe the pattern of evolutionary change in behavior. Consider a recent example:[2] if we tickle a human or a great ape (Chimpanzee, Bonobo, Gorilla, Orangutan), one motor pattern that we elicit is laughter. Although the motor pattern is obviously "the same thing" in the five species, there are clear differences. When researchers constructed a family tree of the five species based upon measurable aspects of the laugh sounds that they recorded, they arrived at the

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[2] Davila-Ross, M., Owren, M.J. & Zimmermann, E. 2009. Reconstructing the Evolution of Laughter in Great Apes and Humans. *Current Biology* 19, 1106-1111.

same tree that one gets by comparing anatomy, or amino acid sequences of proteins, or nucleotide sequences of DNA. Orangutans branch off first, then Gorillas, leaving Humans, Chimpanzees, and Bonobos clustered together and only recently diverged from each other. We can also trace evolutionary change in the laugh sounds. For example, when humans laugh, there is repeated voicing on exhalation followed by silent inhalation: HA-breathe in-HA-breathe in-HA-breathe in-HA. As Chimpanzees diverged from humans, they increased the tendency to voice on inhalation and exhalation. Try it: say HA as you breathe out and as you breathe in: you will sound like a Chimpanzee being tickled.

Tinbergen also noted that if behavior has, in his words, “survival value,” meaning that it is specialized to fit the animal to its species-specific environment, then the behavior must have reached its current form through evolution by natural selection. For example, imagine a population of geese in which the egg rolling motor pattern, because of a recent change in the vegetation where the geese build their nests, has a 70% success rate. Seven out of ten eggs that roll out of the nest are successfully retrieved. Further imagine that there is individual variation in egg rolling in the population. Some rare individuals roll more effectively in the new nesting habitat and they have a 90% retrieval rate. Those individuals will rear more young than the 70% retrievers. Finally, imagine that the individual differences in egg rolling success are in part due to genetic differences among individuals. After just a few generations, the genetic makeup of the population will be different, with more individuals having the efficient egg rolling genes and hence the efficient phenotype.

Charles Darwin was the first person to fully grasp the notion that adaptation, the fitting of a species to its environment, must happen in this way, and he coined the term natural selection to refer to the process.

You may now be objecting that I asked you to imagine a lot. To conclude that there was evolutionary change in behavior by natural selection, we had to make quite a few assumptions. Mainly, we had to assume: 1) that individuals varied in performance, 2) that this variation created differences in reproductive success, and 3) that the variation was in part due to genetic differences among individuals that could be reliably inherited. Tinbergen argued that we needed to study these things. How does the genetic control of behavior work? How is behavior inherited? How rapidly can behavioral change occur when there is selection?

Tinbergen's Four Questions were a remarkably complete prescription for the study of behavior, and they also provided an enduring model of organized thought in Biology. His thinking should guide you as you make your way through this book.

Chapter Two

Multiple Realities

Geerat Vermeij, an evolutionary biologist at the University of California at Davis, is the author of a provocative thesis that he calls Escalation. Vermeij's principal work has focused on the evolutionary arms race between bivalves (clams, oysters, scallops), and their predators, such as crabs and drilling snails. A crab attacks a clam by chipping with its claws at the margin where the two sides of the shell open and close. Sufficient chipping breaks the seal between the sides of the shell, allowing the crab its initial entry. A drilling snail sets itself up, like a miniature oil rig, on the side of a clam shell and then uses its radula, a toothed, back-and-forth conveyor belt-like organ in the mouth, to slowly rasp a hole through the shell. When the hole is complete, the snail everts its stomach through the hole to digest and absorb the clam's soft body. Vermeij, working with many fossil specimens, demonstrated clear trends that have occurred over a long sweep of evolutionary time. Clams acquire thicker shells with thicker lips at the shell margin, while the crabs acquire stronger claws and the drilling snails more effective radulae and drilling behavior. Vermeij's term to describe these evolutionary step-for-step changes in predator and prey is escalation, a word taken from the mid-twentieth century lexicon of the U.S. - Soviet nuclear arms proliferation. Vermeij has argued compellingly that the evolutionary patterns he described between clams and their predators is a general characteristic of life. Over evolutionary time, life inexorably becomes more dangerous and competitive, as organisms become better defended and more effective at competition and predation.

Insects escape many of their would-be predators by simply flying away. Flight in insects likely evolved in response to a world made increasingly dangerous by insect-eating animals. Then a descendant group of the dinosaurs, the birds, also evolved flight, and insects became the main menu item for many bird species. The significance of insects in the diets of birds is revealed by the fall and spring migrations of hundreds of species of birds. Migration between the Northern and Southern Hemispheres evolved because spring migrants to the North find a superabundance of insects in spring and summer. Some insects have escaped bird predation by an evolutionary change in their daily activity schedules; they rest during the day and become active only at night, when birds, that hunt using vision, cannot see them. As a result, a huge potential advantage appeared for any animal group that could evolve the ability to exploit the insect-filled nighttime air. Into this huge vacant niche stepped a group of tiny mammals: the bats.

Seeing with Ears

Unlike birds, mammals were already nocturnal, so the bats had only two remaining changes to make: develop flight, and develop a way to see in the dark. The bats did both, and in consequence they became the second most successful mammal group (the most successful group is the rodents). Most bats fly at night and pluck insects out of the air. The fact that there are so many bats (many species, and, within species, often millions of individuals) means that they are very accomplished at this seemingly impossible task. In the mid-twentieth century, biologists who wanted measure just how accomplished bats are took a direct approach: they shot individual bats at known times after evening emergence and weighed the stomach contents. The reason for measuring feeding rate was to settle the question of whether bats can "see" their prey or whether they simply fly through the insect-filled air with open mouths[3]. The results gave a conclusive answer. Generally, within about an hour after emerging from its daytime roost, a bat has packed its stomach with a mass of insects equal to about one-fifth to one-third of its own body mass. This far exceeds the abilities of human competitive eaters, who win contests by consuming 4-5% of their own body mass while sitting down, not flying. Given the average mass of the individual insects that bats eat, the total mass consumed means that a bat catches about 500 insects per hour, or one insect every seven seconds. These figures imply two things. First, the night air is full of insects, many of which are quite tiny. Second, bats are extraordinarily efficient at plucking these tiny prey out of the air. Some simple calculations showed that the capture rates cannot result from a bat simply flying with its mouth open. Rather, the bats are detecting and then pursuing and capturing individual insects.

Although bats act as if they are able to see insect prey in the dark, as well as to see obstacles and other features of the environment through which they fly, they have tiny eyes and weak vision, which an optometrist would measure at about 20/400. The phrase "blind as a bat" is reasonably accurate. Thus, as early as the Eighteenth Century, biologists began to postulate that bats might somehow be able to "see" with their ears. However, real proof that bats do indeed see with their ears came only in the mid Twentieth Century. The proof resulted almost entirely from the brilliant efforts of a single man, Donald Griffin, who combined the observation of bats in nature with new technology that allowed him to detect

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[3] Gould, E. 1955. The feeding efficiency of insectivorous bats. *Journal of Mammalogy 36, 399-407.*

and to record the sounds, inaudible to humans, that bats produce. Griffin discovered the sensory process known as echolocation.[4]

Humans gained a new perspective on their environment when images of the Earth from space became available. Suddenly, the gossamer nature of the gas film that sustains us became distressingly obvious. Just 60 miles up, the air ends and outer space begins. Even at 20 miles up, the density of the air is one one-hundredth of the density at the ground. That distance, 20 miles, is two-tenths of one percent of the diameter of the Earth. The Earth, by most human reference standards, is a massive object, but gravity is a very weak force. Thus, the Earth holds on to only a thin veneer of gas, which we call the atmosphere. At the Earth's surface, the weight of that 60 miles of gas creates atmospheric pressure, which presses evenly on things from all directions.

What we call sound is our sensory interpretation of wave energy that propagates through the atmosphere at about 343 meters per second. A sound wave is produced by the vibration of an object in air. You can produce a visual representation by dripping discrete drops of water into a pool of still water: the waves propagate out from the source of disturbance in all directions. Depending on the size of the drops and the height from which you drop them, the waves will have a specific height, or *amplitude.* Depending on how rapidly you let the drops fall, the waves will have a specific distance from crest to crest, or

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[4] Griffin, D.R. 1958. *Listening in the Dark. The Acoustic Orientation of Bats & Men*. Yale University Press, New Haven. This now classic book is a fascinating account of the detective story-like process in which Griffin made the discoveries to prove that bats use echolocation.

frequency. When a sound wave passes by a place, the local air pressure rises slightly and then falls back to atmospheric pressure.

In the terrestrial mammals, the hearing sense operates by detecting the tiny transient fluctuations in atmospheric pressure that are produced by sound waves. Differences in amplitude are perceived as differences in loudness, and differences in frequency are perceived as differences in pitch. The pressure changes are detected by the eardrum, a thin membrane that is the only barrier between the back of the throat and the atmosphere. The Eustachian tube, an evolutionary remnant of the soft tissue skeleton of fish gills, provides the connection between the back of the throat and the inside of the ear drum. Because air pressure in the throat is atmospheric pressure, there is atmospheric pressure on both sides of the eardrum at rest. This allows the eardrum to register the tiny transient changes in atmospheric pressure created by sound waves. Resting against the inside of the eardrum is a chain of three little bones, the Malleus, Incus, and Stapes. Vibration of the eardrum is passed along the chain of bones to a membrane on the cochlea, the tiny conch shell shaped organ of hearing. I will not go into specifics of how the cochlea works at this moment. I will simply note that the cochlea is where patterns of mechanical vibration are transduced into patterns of activity in the auditory nerve, that carries the information to the brain. The cochlea is the principal bit of anatomy where the auditory sensitivity characteristics of a species are created. For any species, hearing physiologists can construct a tuning curve, where sound frequency is represented on the X axis and the minimum sound pressure at which a response from the cochlea can be detected is on the Y axis. A tuning curve shows the range of frequencies that a species can hear and the range of frequencies that a species hears best. Tuning curves usually have the shape of a shallow U. For Humans, the tuning curve shows the ability to hear sounds from 20 to 20,000 Hz (Hz = Hertz, or number of wave crests per second) with the bottom of the U, the most sensitive hearing, centered at 2000-4000 Hz, a region where most of the energy in human speech sounds occurs. For bats, the curve shows the ability to hear from 20 to 120,000 Hz, with the greatest sensitivity at 40,000-80,000 Hz.

Bats are able to hear very high frequency sounds because they produce such sounds to echolocate. A bat that has emerged from its roost, flying at perhaps 20 meters above the ground, emits a series of clicks. Like all mammal voices, the clicks are produced in the larynx. Each click is of short duration, about 0.0012 seconds, is very loud, about 110 decibels, a sound pressure equivalent to that produced by a jackhammer breaking up pavement, is very high pitched, at about 40,000 - 100,000 Hz, and typically is a glissando, with a steep frequency drop of 30,000 Hz or more. Griffin referred to these short, loud, high pitched, frequency-modulated screams as cruising pulses. A cruising bat emits these at a rate of about 8 per second. While the bat is screaming, it protects its own hearing by contracting muscles that pull sideways on the Malleus and the Stapes, partially unhinging the chain of ear bones. Then the bat turns its ears back on and listens for the echo of its scream, using the information present in the echo to produce a picture of the immediate surroundings.

The chirps are optimally designed for echolocation in a number of ways. First, the frequency range puts the chirps into a proprietary communication channel. There are no other naturally occurring sounds in this frequency range (other than the howling of some mice on the ground). High frequencies attenuate rapidly in air, so the bat cannot be distracted by echos that come from beyond the immediate vicinity. High frequency also allows the bat to collect information from the echo that it can process to build a picture of the texture of the object from which the echo bounced. Second, the chirps are brief. This allows the bat to sense the distance to an object by calculating an accurate time between the outgoing chirp and the return of the echo. Third, the frequency modulated portion of the chirp provides even greater resolution in distance estimation. This point may require some explanation. Imagine that you emit a constant-frequency chirp, at 40,000 Hz for a duration of one second. You listen for the returning echo. To compute the distance to the object that bounced the sound back, you need to measure the time between your production of the sound and its return. The echo comes back one-fourth of a second later, but the entire one second of sound does not come back: because of degradation of the sound in atmosphere, only one-half of a second of the sound comes back. Now, you probably see the problem: you don't know whether the fragment that came back is an echo of the first half second of your call, the last half second, or some part in the middle. So your estimation of distance will be imprecise. But, if your chirp is not constant frequency, but a steep glissando, then each outgoing frequency has a distinct time stamp, and even a fragment of an echo will indicate time, and hence distance precisely. Fourth, most chirps have a short constant frequency bit that precedes or follows the frequency modulation. A comparison of the frequency of this part of the chirp to the frequency of the return echo allows the bat to detect Doppler Shift, and hence the relative velocity of the sound reflecting object.

When a cruising bat detects an object of interest (perhaps a moth, perhaps a spitball shot into the air with a glass tube blowgun by Donald Griffin), it flies in that direction, begins to increase its click rate and to shorten the duration of each click, building pictures of the immediate environment at a faster and faster rate. as the bat closes on the insect, it emits what Griffin called a buzz, in which each click lasts just 1 millisecond and clicks are emitted at 200 per second.

Biologists continue to make discoveries about the capability of the bat echolocation sense[5], have had some success in working out the general algorithms by which echo processing occurs, and have mapped the brain areas that receive and process information from the auditory nerves. Thus, we now know enough to address the Eighteenth Century conjecture that bats must "see" with the ears. The conjecture was in essence correct. Bats do indeed have a sense that works in the dark and that rivals the detail provided by vision.

What would this sense feel like if we possessed it? We can only guess, like a congenitally blind person trying to imagine what vision feels like. Bat echolocation illustrates the point that I want to make in this chapter. The point is that each animal species has its own sensory tuning and sensory processing abilities and hence its own reality. The realities of species can be represented as sets. The degree to which the sensory sets of two species overlap is governed primarily by their evolutionary relatedness. The smaller the amount of

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[5] Bates, M. E., Simmons, J. A. & Zorikov, T. V. 2011. Bats use echo harmonic structure to distinguish their targets from background clutter. *Science* 333, 627-630.

time since the evolutionary divergence of two species, the more similar their realities will be. For animals there is no single reality.

For millennia, philosophers mused about the nature of reality and of consciousness. They sought to discover the truth by simply thinking about it. They made slow headway, and for millennia, theirs was the only game in town. Finally, in the past two centuries, empirical science has finally amassed enough knowledge to be able to offer an alternative view. That view is that there *is* a single physical Reality in the universe. Animal life, in its inexorable trend to become more competitive, more efficient, better at harvesting energy and materials and converting these into offspring, has evolved senses, structures that are sensitive to some parts of Reality and transduce this into patterns of nerve signals. The senses that animals have acquired are those that: 1) are physically possible, and 2) provide the animal with useful information that it needs to survive, compete, and reproduce. Animals do not sense parts of Reality that are not useful in these pursuits. Gathering information is important, but ignoring irrelevant information is equally so.

Moth Ears

Inattention to irrelevant information is exemplified by many nocturnal moths that are pursued by bats. These moths have evolved an ear which consists of an eardrum on each side of the body below the wings, and exactly two nerve cells per side that report to the moth's brain. This simple ear has a flat tuning curve across a wide frequency range from 20,000 to 100,000 Hz. This is the range of bat echolocation clicks. The moth does not, in effect, care which sound frequencies are present, and it does not hear sounds below 20,000 Hz. The only information that the moth requires is to know if a bat is nearby and, if so, how close. The simple ears allow a moth to detect a bat at a range that is greater than the range at which the bat can detect the moth, and the two nerve cells per ear also provide enough information on the location of the bat. A moth that makes such an early detection (the nerve cells of the ear toward the bat will be active and the nerve cells of the contralateral ear will not) turns abruptly and flies directly away from the bat. If the moth is detected by the bat, its ears report that the echolocation clicks are now louder and are coming at a faster repetition rate. Beyond a certain threshold, the moth's response abruptly changes and now it drops to the ground, but in an erratic chaotic way that make its flight path unpredictable.[6] Although they are adversaries locked in an escalating predator-prey struggle, bats and moths could not have more dissimilar auditory realities. For bats, auditory processing provides a rich, vision-like picture of the immediate surroundings in the nighttime air. For moths, auditory processing is like the check oil pressure light in an automobile dashboard.

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[6] Roeder, K.D. 1962. The behaviour of free flying moths in the presence of artificial ultrasonic pulses. *Animal Behaviour* 10, 300-304.

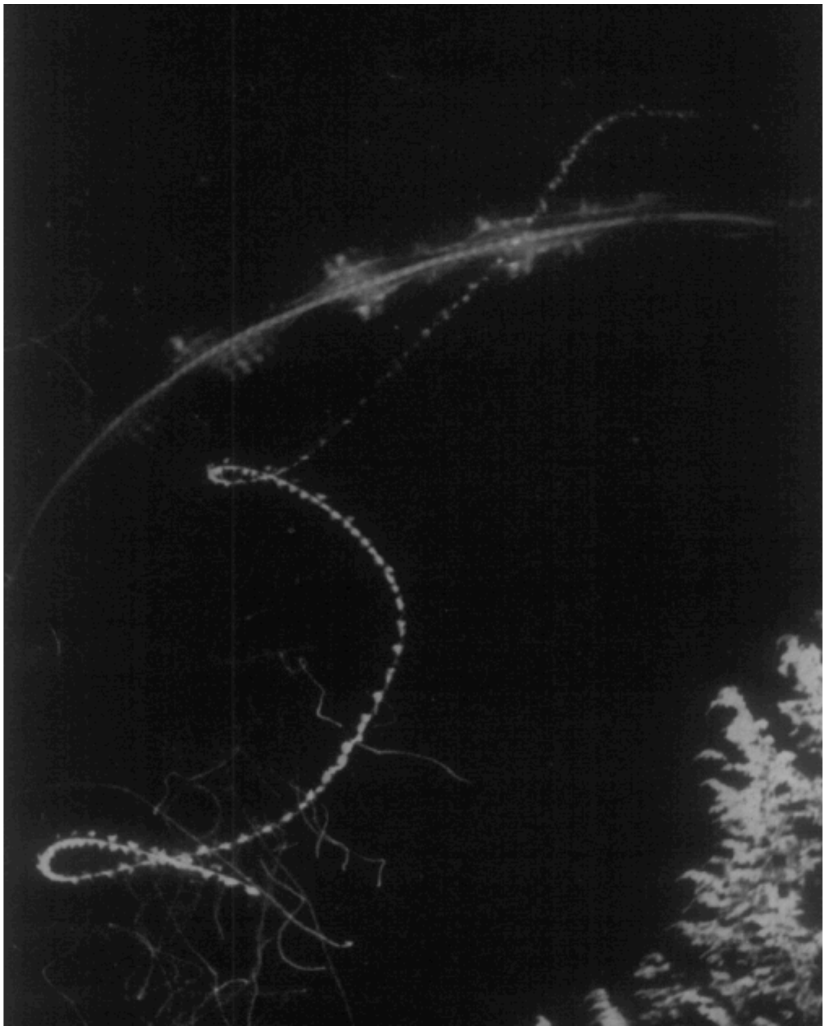

Figure 2.1 - An instant in the summertime night sky captured by Ken Roeder. The fighter jet like arc indicates the path of a foraging bat. The looping chain indicates the path of a moth that detected the close approach of the bat and initiated its chaotic descending escape. The faint traces are those of other insects.

Fly Eyes

Eyes are sensory structures that are adapted to transduce light energy into useful patterns of nerve activity that the brain can use to build an accurate representation of the environment. Light is electromagnetic radiation, which has both particle and wave characteristics. The wave characteristics allow us to characterize types of electromagnetic energy by wavelengths, the distance from one wave crest to the next. What we perceive as visible light has wavelengths from 400 to 700 nanometers (a nanometer is one-billionth of a meter and is abbreviated as nm). At wavelengths shorter than 400 nm are forms of radiation called ultraviolet, X-rays, and Gamma Rays, with wavelengths down to 0.01 nm. At wavelengths longer than 700 nm are forms called infrared, microwave, and radio wave, with wavelengths up to 1,000 meters or more. Animal eyes have evolved sensitivity to electromagnetic radiation in the narrow band that we call visible light because this range represents the majority of solar radiation that reaches the Earth, and because radiation in this range can provide useful information about objects in the environment. Like sound waves, light bounces off of objects and thus provides information about what is out there. Because light travels *much* faster than sound, and because light has such small wavelengths, it represents an incredibly rich source of information. More than any other sense, light provides highly detailed, accurate information about the presence of objects, their motion, and their positions as we move near them. A peregrine falcon may reach speeds close to 90 meters per second as it dives at prey, but light travels at about 3 hundred million meters per second, so the falcon’s eyes give completely accurate reports about the closing distance.

All animal vision operates in the same basic way. Light sensitive cells in the eye contain visual pigments, molecules that undergo a structural change when they absorb a photon, the particle unit of light. The shape change starts a chemical cascade that results in the production of a nerve signal. Among animals, variety in the specific wavelength sensitivity of visual pigments and in the optical equipment that delivers light to the pigments produces variety in visual reality.

All vertebrate animals (animals with a vertebral column, or backbone: fish, amphibians, reptiles, birds, mammals) have the same basic visual equipment. They have two spherical camera-type eyes, with a pupil to admit light, a lens to focus images on the photosensitive retina, muscles that deform the lens to focus at different distances, and six muscles that rotate the eye in its socket. The ability to discriminate between different wavelengths of light and thus to perceive what we call color depends on the variety of visual pigments found in the calls of the retina. Most of the vertebrates have more kinds of visual pigments than we do, and thus they see more colors, including colors into the ultraviolet.

The other major eye design of animals exists in the arthropods: the spiders, scorpions, centipedes, millipedes, lobsters, crabs, shrimp, and insects. The arthropod body plan features a rigid external skeleton called the cuticle, with jointed limbs, and muscles that pull across these joints from the inside. This is the winning body plan. Over 80% of known animal species are arthropods. Most arthropods see with what is called a compound eye. A compound eye, such as the eye of that housefly that you crushed, is composed of several thousand individual units called ommatidia. Each ommatidium is a long, slender tube with an exterior lens and interior cells that contain light sensitive pigments. Imagine a closely packed bundle of drinking straws with one end of each stuck into a baseball-sized lump of clay. Each straw will point in a specific direction. Because the compound eyes of arthropods often make up more than one-half the surface area of the head, an individual animal has ommatidia that point in almost all directions. Thus, even though your hand approached the fly from behind, she detected you easily.

The compound eye is more democratic than the vertebrate camera eye, with its dominant fovea, the area where receptor cells are packed closely together and where interpretive representation in the brain is rich. In the vertebrate eye, activity in most of the retina, away from the fovea, is mostly used to tell the brain whether there is something worth pointing the fovea at. The vertebrate eye throws away a lot of information to gain the very high image resolution that the fovea creates. In contrast, the compound eye gives equal representation to the output from each ommatidium. The resulting view of the world is thus something like a pointillist wide screen IMAX. But, as when trying to imagine what echolocation feels like, we can only guess what the visual experience provided by a compound eye would be. We do know that the compound eye is superbly good at detecting motion and that it has a very high flicker fusion frequency. A DVD shows separate images at 25-29 per second; with the low flicker fusion provided by our camera eyes, we perceive this as uninterrupted motion. Florescent lights flash 120 times per second under the rapidly flip-flopping polarity of Alternating Current. A housefly sees the separate flashes. She is so good at detecting motion that you can only get at her with the raw speed provided by your fly swatter.

Detecting a Buried Flounder

We can go further into the realm of the unimaginable by considering the ability of some animals to detect electric fields. The sharks and rays use this sense to find prey and possibly to navigate. On the snout, around the mouth, and above and blow the eyes of these fish is an array of clearly visible dark pits. The short pits, open to the surrounding water, are filled with a jelly like material and have receptor cells at the bottom. These are the Ampullae of Lorenzini, first described by Stefano Lorenzini in 1678, but not proven conclusively to be electroreceptors until 1971.[7] The receptors detect voltage differences between the pore opening and the base, and they are extraordinarily sensitive. They are able to detect a difference of one hundred millionth of a volt at one meter. Because the heart, breathing muscles, and skeletal muscles of animals produce small electric fields (recall from Chapter One that we can use EMG to detect when a muscle is contracting), a shark can detect a flounder, motionless and buried beneath the sand, at a distance of 30 centimeters. The sensitivity of the Ampullae of Lorenzini is also sufficient to allow sharks to detect the direction of the earth's magnetic field.

In the muddy, murky rivers of the Amazon basin and of central Africa, two distantly related groups of fishes have taken electroreception to another level. These animals perform the electrical equivalent of bat echolocation. These so-called weakly electric fish use specialized blocks of muscle to produce an electric field around the body; they then detect

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[7] Kalmijn, A. J. 1971. The electric sense of sharks and rays. *Journal of Experimental Biology* 55, 371-383. This is a classic investigation and a great read.

disruptions in the field. When it is near to an object, the fish experiences a kind of electric shadow that falls on the body, and it uses this information to build a picture of the immediate environment. The weakly electric fish also communicate with each other using pulsed electric discharges.

Because we have hearing sense, we can at least roughly imagine what echolocation must be like, and because we have vision, we can similarly imagine what it is like to see with a compound eye. Electrical sensitivity seems completely alien. The closest sense that we have probably is touch. Imagine your sense of touch extending out several feet away from your body.

Map and Compass

Another sensory mode for which we have no intuitive feel is found in many animals that perform long distance homing. My house is located on a small forested hill in northern Idaho. Each spring, a rufous hummingbird tells me that it is time to put up the feeder by hovering at the spot where the feeder will hang. This bird has come several thousand miles from southern Mexico where it spent the winter to the exact spot where it guzzled the sugar water that I provided the previous summer. This extraordinary long-distance homing accuracy is not unique. In all species that have evolved long distance displacements as part of the life history, senses that provide both map and compass information exist. One of those senses involves the ability to detect the earth's magnetic field. The nature of the magnetic detectors and the mechanisms by which these detectors transduce magnetic field forces into patterns of nerve signals is still being worked out. Nevertheless, it is now quite well established that if we alter the magnetic field around an animal that is homing (some early experiments involved glueing a bar magnet to the heads of homing pigeons), we alter the compass direction of the animals homing movements. If we make the right kind of magnetic field adjustment, in some instances it seems that we alter the animal's perception of where it is with respect to home. Thus we know that some animals can perceive some aspects of the earth's magnetic field. The fact that we humans rely so heavily on the GPS system is evidence of how magnetically blind we are. Our magnetic blindness explains why the discovery of this ability in animals did not happen until the mid twentieth century. Magnetic blindness in humans is not surprising, because we did not evolve as a migrating, homing species. Each animal species evolves the senses that are appropriate to the tasks that individuals perform to survive, compete, and reproduce.

Tactile Foveation

I mentioned that our camera eyes solve the problem of processing abundant information by assigning to most of the retina the menial task of reporting whether there is something to look at, while assigning to a small area of the retina, the fovea, the job of analyzing the detail of images. In the fovea, light receptors are packed together at high density. There is a correspondingly large area of the visual brain that is dedicated to processing signals from the fovea. Thus, our eyes almost constantly make small twitching adjustments to point the fovea at specific spots in the field of view. These movements are called saccades. We do not notice the saccades of other people because the movements are small and quick: the typical duration is 3-6 one hundredths of a second.

A similar kind of sensory processing, the devotion of one part of a sensory apparatus to detailed analysis and the use of the remainder of the apparatus to identify analysis targets, occurs in a burrowing mammal, the star-nosed mole. Like other moles, this species is adapted to find and eat subterranean invertebrates. Moles use their powerful forelimbs to swim through soil, constructing a burrow system which they can patrol for food. Within this narrow, specialized niche, star-nosed moles have become even further specialized; their diet consists of underground food items that are also tiny.

Eating tiny food items is an effective feeding strategy only if the time spent collecting and eating each food item is very brief. What counts in the economy of nature is the rate of energy of acquisition, the calories consumed per second of foraging. Imagine a species that eats small food items that are on average 1 gram in size. If an individual of this species eats 10 food items, taking 1 second to find and consume each item, its rate of food consumption is 1 gram per second. Now consider another species that eats large food items, of average size 10 grams. The large food items are more dispersed than small food items, and consuming a large item requires more time than consuming a small item. Let's say that individuals of this second species on average need 20 seconds to find and consume each item: the rate of food acquisition is one-half of a gram per second. Thus it is possible for a species to become a specialist at eating tiny food items, but only if its so-called "handling time" per item is brief. For example, a blue whale, the largest living animal on earth, eats tiny food items. The whale achieves a small handling time by taking a volume of sea water the size of a school bus into its mouth, and then pushing the water through its baleen plate, leaving behind a few million planktonic plants and animals to swallow.

However, this mass filtering strategy is not available to an animal that swims through soil. Star-nosed moles find and consume prey items one at a time, so if they are to specialize on tiny food items, the handling time for each item must be extremely brief. The moles achieve really fast handling times by touch, using the unique stars on their noses. A star-nosed mole has a slightly upturned snout. Surrounding each nostril is a crown of fleshy tentacles, that are studded with thousands of touch receptors. The bottom tentacle, number 11, that rests just above the mouth, is the touch equivalent of a fovea. The area of the brain that processes the signals from this tentacle is much larger than the areas that are devoted to the other tentacles.

Figure 2.2 - A star-nosed mole. Photograph courtesy of Ken Catania.

Figure 2.3 - Scanning electron micrograph of the star. Each individual bump is a touch organ. Photograph courtesy of Ken Catania.

When the outer tentacles of the star touch a potential food item, that item is brought to tentacle 11 in an extremely rapid movement that is as quick or quicker than a saccadic eye movement. This rapid evaluation creates an average handing time of about 2 tenths of a second, making it possible for star-nosed moles to be small food item specialists[8]. Over one-half of the star-nosed mole's somatosensory cortex, the brain area that is devoted to the analysis of nerve reports from touch receptors, is occupied by areas that process information from the star.

The Sensory World of a Tick

I will close the discussion of multiple realities with a description of the sensory world of a female tick. A female tick needs a meal of mammal blood to provide the nutrition that is required for her eggs to mature. So, a female, having found an elevated perch on a blade of grass, becomes senseless to everything in her environment except a single chemical compound. She may wait, motionless for a decade or more, ignorant of the rising and setting sun, breezes, coyotes howling, birds singing, rain and snow, and the apparent passage of time. All of her senses except her chemical sense are turned off, and her brain is waiting for a single signal from her chemical senses that indicates the detection of a 4-carbon carboxylic acid: butyric acid. To us, butyric acid is a powerful odor. The compound is one of the salient constituents of unwashed armpit odor, and it is produced in the glands at the base of hair follicles in all terrestrial mammals. Butyric acid is an infallible indicator that a mammal is close by. When the female tick perceives this compound, she jumps. If she is fortunate, she lands on the mammal. Now she loses her sensitivity to butyric acid and

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[8] Ken Catania of Vanderbilt University, a recipient of the MacArthur Award, figured out what the moles do with their stars. See: Catania, K. C. & Kaas, J. H. 1997. Somatosensory fovea in the star-nosed mole: behavioral use of the star in relation to innervation patterns and cortical representation. *Journal of Comparative Neurology* 387; 215-233; Catania, K. C. & Remple, F. E. 2004. Tactile foveation in the star-nosed mole. *Brain, Behavior and Evolution* 63: 1-12; Catania, K.C. , Remple, F.E. & Fiona, E. 2005. Asymptotic prey profitability drive star-nosed moles to the foraging speed limit. *Nature* 433: 519-522.

gains sensitivity to heat. By moving up a gradient toward hotter temperatures, she reaches the skin, where she will find her blood meal. For a tick, reality is contracted to the perception of just three stimuli: light which directs her initial climb, butyric acid, which releases her jump, and heat, which guides her to the skin.

At the beginning of the Twentieth Century, a German biologist, Jacob von Uexkull used the example of a female tick to support his thesis that each animal species, because of its particularly designed and tuned sensory system, has its own sensory world, its own *Umwelt*. What we have learned about the sensory worlds in the century since van Uexkull has verified his fundamental insight. Each species really does have its own *Umwelt*, its own perception of reality, that provides individuals with the information that they need to survive, compete, and reproduce, and, just as importantly, excludes the information that is irrelevant to these goals. There is a single Reality, but no animal species perceives all of Reality. Even all animal species, taken together, do not perceive all of Reality. Some parts of Reality are just not useful to an organism that is trying to harvest energy efficiently, to maximize the number of offspring that it can produce.

Chapter Three

Adjusting Priorities

In my first sabbatical year, my wife and our two children, aged one and three years, and I went to Australia. I wanted to study the play behavior of marsupials, and if you want to study marsupials, Australia is the place to go. To accomplish the kind of survey that I had in mind, I needed to observe juveniles of species that were representative of as many different marsupial groups as possible, and this required that we travel. In the closing months of my study, we moved from Melbourne to Cairns, where I wanted to observe several species, from the groups known as possums and gliders, in the wild. In Cairns, I met Rupert Russell, a naturalist who had studied several species of possums and gliders for many years[9]. Rupert graciously introduced me to his study site in the Atherton Tablelands above Cairns and he showed me how to watch the gliders.

One method of observation is to focus on the sap trees that the large yellow-bellied gliders tend and harvest. Within its territory, a group of yellow-bellied gliders selects a few specific trees to mine for sap. Using their teeth, the gliders cut incisions in the bark and come back later to lick the sap that oozes out. A yellow-bellied glider sap tree is studded with hundreds of bumpy incision sites, and it attracts other glider species, so it is a convenient place to make observations.

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[9] Russell, R. and Russell, K. 1980. Spotlight on Possums. University of Queensland Press, St Lucia, Queensland.

Like many Australian marsupials, the gliders have traits that are essentially identical to traits found in placental mammals on other continents. Biologists refer to this kind of resemblance, in which species in unrelated groups independently evolve the same adaptations, as convergent evolution. In North America, the gliding placental mammal is a rodent, the flying squirrel, which is also a sap miner. Flying squirrels and Australian gliders have a flap of skin that extends from the forearm to the shin. By assuming a prone, spread-eagle position, these mammals can sail from tree to tree in sloping, controlled descents. They don't flap and they don't really fly, but they can descend at a shallow angle and so can get around quickly from tree to tree. Gliding also keeps them out of the clutches of predators that hunt on the ground.

Rupert showed me the sap trees and the nest trees of the yellow-bellied glider group that he studied. At dusk, I sat at the base of a tree about 120 meters from the nest tree and with binoculars watched the gliders emerge to sit on a branch high above the ground, silhouetted against the darkening sky. Then, when it was almost too dark for me to see, a glider leapt from the branch and sailed, arms and legs outstretched, banking occasionally to dodge projecting branches, toward me. Rupert had also shown me the tree that was the glider's first way station on their route to a sap tree. The glider lowered its feet to bank upward and to drop speed as it neared its first target, hitting the tree about 3 meters off the ground, just above my head. It then ran up the tree to gain elevation and took off on a new glide. The entire group could reach the first sap tree, about 500 meters from the nest tree, in just a couple of minutes. Then, as long as I walked without scuffling leaves, I could turn on my red headlamp, approach the sap tree, and watch the juveniles in the glider group. A few hours later, after the gliders left, I would walk back to camp. There, I would take off my shoes and socks to remove the leeches that had attached between my toes. Sometimes, a leech or two would have attached to my leg, as well. When I pulled the leeches off and flicked them away, the sites where they had been attached bled spectacularly until the leech anticoagulant saliva had washed out.

My family accompanied me on one of my trips to watch the gliders, and they all experienced the leeches. My three year-old daughter Anna was at first frightened by these black, inch long worms that stuck to your legs and left such a vivid stream of blood when you pulled them off. Then I explained to her that the leeches weren't dangerous and that they were holding on only by sucking - contracting a circular ring of muscle around the mouth. I explained to her how the leech has to attach first with this anterior sucker before it can use the super-sharp cutting plates in its mouth to make an incision that you don't feel. Then, once she had learned how to pinch a leech's head to break the seal, Anna began to play with a leech. She held it against her arm and it attached. Then, before it started to cut, she pulled it off. Then she held it against her arm again, and the leech attached. With the patience of a child, she showed that a leech, presented with the stimulus of warm mammal skin, initiates the attaching motor program, even when it has just been pulled off after attaching to a little girl's arm for the twenty-fifth time.

The behavior of the leech that Anna delightedly manipulated was entirely machinelike and stimulus-driven. Was this simply a stupid leech, or are all leeches unusually dim? Far from it. Most animals have relatively small brains, that can provide for nothing more than machinelike reactions to stimuli. The great French naturalist Jean-Henri Fabre (1823-1915), an early pioneer in the study of insect behavior, described many examples of the apparent wisdom but also the stupefying rigidity of behavior that is produced by pencil point-sized brains. Fabre made detailed observations of the nesting behavior of a number of species of digger wasp species. When she is ready to lay an egg, a female digger wasp excavates a tubular burrow in soil. She then hunts for prey, such as a cricket. She stings the cricket at a place in its ventral nerve cord, inducing paralysis. The wasp is quite specific about the placement of her sting. The goal is to produce paralysis, not death. She then drags the living cricket head first into her burrow, and lays an egg at the base of one of the cricket's legs. She exits the burrow, scrapes sand and pebbles into the burrow mouth to seal it, and flies away, never to return. Underground, the egg is in a safe position on the cricket's body, where it can't be injured, even if the cricket wakes up a bit and struggles against the close confines of burrow walls. The egg will hatch and the wasp larva will eat the fresh meat of the paralyzed but living cricket. The cricket will provide many meals. When it has consumed the cricket and grown sufficiently, the larva will pupate, going through that second, reorganizing phase of development that is characteristic of many insects. Still underground, it emerges from its pupal case as a new adult wasp that will dig to the surface.

Fabre performed the following experiment with a wasp in his home laboratory. While the female was kicking sand to fill a burrow that she had just provisioned, Fabre pushed her aside and used a knife and forceps to clear the partially formed burrow plug. He then removed the cricket with the single wasp egg glued to the base of a leg, and put the cricket in a box. The female wasp stood nearby while Fabre did this. When Fabre took his hands and instruments away, the female entered the burrow, emerged soon after, and resumed the plugging operation. When the plug was complete, she flew away. Although the female obviously had the opportunity to perceive that the cricket and her egg were no longer in the burrow, she continued with the behavioral sequence where Fabre had interrupted it. With this and with hundreds of other experiments, Fabre illustrated how insects, with their tiny brains, can exhibit complex, goal directed behavior that looks like it involves conscious planning and intent. Complex sets of acts, such as digging, provisioning, and sealing a burrow are caused by a chain of instinctive responses. The stimuli that indicate the completion of one task in the chain initiate the next set of responses. Once a female has switched into the next sequence, she can't stop, and she can't go back, as Fabre illustrated.

To us, with our huge brains that allow for behavioral adjustments to contingencies, it seems remarkable that such rigid programming works to guide an animal through its life in nature. Even Charles Darwin, a staggering intellect who thought deeply about natural history, was troubled by the apparent wisdom of instinct. When we consider that, in modern insects, we see the result of over 300 million years of slow tinkering and improvement by natural selection, the apparent perfection of behavior that is achieved by rigid responses becomes a little easier to understand. But rigid programming can only prepare an animal to respond appropriately to the environment in which the programming evolved, as illustrated by Fabre in his laboratory, or by a curious little girl with a leech, or by you with your fly swatter.

Rigid, instinctive responses are also found in animals with relatively larger brains. The phenomenon of brood parasitism in birds provides an example. Brood parasites are bird species that rely on other bird species to rear their young. A brood parasitic female, such as a cuckoo or a cowbird, searches for the nest of an appropriate host species. The parasitic female lays an egg in the host nest and departs. Host parents generally don't seem to notice that a new egg is present in the nest. The parasitic species' egg usually hatches first, and in some species, such as cuckoos, the newly hatched chick has a rapid instinctive response to other eggs in the nest. It backs up to each egg, maneuvers the egg onto its shoulders, and pushes the egg out of the nest. Host parents may be present when the evictions are occurring, but they do not intervene. Now, there is a single parasitic chick in the nest, and it demands food by cheeping and throwing its beak wide open, just as the host chicks would have done. The host parents respond to this irresistible stimulus by feeding the parasitic chick. Even when the parasitic chick has grown to be larger than the host parents, the parents work valiantly to keep up with its food demands, standing on tiptoe to stuff food into its open beak. Nest parasitism has evolved in many different species because of the predictable rigidity of a bird parent's response to a begging chick.

In populations where the same brood parasites and host species have coexisted for many generations, evolutionary escalation typically has occurred. Host parents become better at recognizing a new egg and if they detect this they may remove the egg or, more likely, abandon the nest. Parasites in response become more circumspect. They wait until the nest is not attended, they remove one host egg before they lay their own, they lay unusually quickly, and their eggs are mimetic: they resemble the size and coloration of the host eggs.

In some populations, parasite parents show what has been termed Mafia behavior[10]. They monitor the nests where they deposited an egg. If the host parents remove the egg, the parasite parents retaliate by destroying the nest. However, the arena of escalation is all pre-hatch. Once there is a begging parasitic chick in the nest, the parents are trapped, resigned by their unvarying response to the stimulus provided by a begging chick into a reproductive season wasted in the service of another species.

At this point, you may be thinking that I was able to come up with an example of rigid responses to stimuli in birds because birds are, well, birdbrained. Bird brains need to be small and lightweight to meet the demands of flight. I can meet your objection with an example from the animal species that has the largest brain in relation to body mass - humans.

The World Health Organization in 2010 estimated that, worldwide, one billion people are overweight and 300 million of these are clinically obese. In the USA, some states have obesity rates greater than 30%. People become overweight and obese because they cannot resist the stimuli that are presented by food. Far too often for their own well being, humans respond to the presence of calorie-dense food (food with high sugar and/or fat content) by reaching for the food, putting the food into the mouth, chewing, and swallowing. They do this despite the loud and clear admonitions of the health professions, considerable social opprobrium, and a glamor industry that extols human stick figures.

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[10] Hoover, J.P. & Robinson, S.K. 2007. Retaliatory mafia behavior by a parasitic cowbird favors host acceptance of parasitic eggs. *Proceedings of the National Academy of Sciences of the United States of America* 104: 3379-4483.

Obesity rates have risen dramatically in the past 30 years because, increasingly, people are not required to do physical labor, and because the food industry has become much more efficient at the provision of calorie-dense food at cheap prices. For the first time in human history, calorie intake exceeds calorie expenditure for many people. At this moment in history, people are not that different from the leech that Anna held to her arm.

At least contemporary humans do not eat constantly, even though they are surrounded by food stimuli at most waking moments. They do not because of a highly complex set of control mechanisms that regulate eating and fat deposition in mammals. These mechanisms involve nerve signals as well as the levels of several hormones in blood. Although the basic mechanisms that control the response to food stimuli are understood, there are still some details to be worked out. However, it is now clear that humans have set points in the control feedback mechanisms that were appropriate in our evolutionary past, when substances that contained sugar or fat were rare, but are not appropriate when a Big Mac is obtained with very little effort.

The presence of feedback mechanisms that control feeding illustrates another fundamental truth about animal behavior. Animals may be stimulus-response machines in some circumstances, but in many others, they are capable of adjusting priorities so that the response to a stimulus varies. An African lion that has not eaten in 5 days responds to the presence of a zebra by attempting to catch the zebra. The same lion that has just consumed 20 pounds of meat regards the zebra with profound indifference.

When an adjustable response to a stimulus is advantageous, natural selection can engineer the appropriate control mechanisms. When an adjustable response never provides an advantage, priority control mechanisms do not evolve. If this reasoning is correct, then the ability to adjust behavioral priorities should not be constrained by the size of the brain. Instead, adjustment should occur whenever the environment provides reliable contingencies that provide a reproductive advantage to the individual that can adjust. There are many illustrative examples of this, which is the primary province of the sub-discipline of animal behavior known as Behavioral Ecology.

How Fat Should a Great Tit Be?

A few species of seed-eating birds, such as Chickadees and Great Tits, have evolved the ability to stay at home during winter. These birds avoid the costs and risks of flying 1,000 miles or more twice each year, but they incur the costs and risks of surviving through a cold winter. A small bird in winter has a real risk of dying each night. During the day, the bird must find and consume enough food to accumulate a fat reserve for the night. While the bird huddles, motionless, it feathers fluffed out to provide as much insulation as possible against the freezing winter night, it uses its stored fat as the energy source to stay warm and alive. In the economy of nature, fat is a good thing. It allows animals to store energy in a very compact form. Even though fat is compact, it weighs something, and weight is always a critical concern for a bird. Each gram of fat that a bird stores is an additional gram that it has to lug around when it walks or flies. There is a transport cost. A heavier bird is also a slower, less agile bird; it is more vulnerable to hawks. Also, accumulating an extra gram of fat means that a bird must be out and exposed to predators while it searches for food. So fat is good in that it allows a bird to survive through a winter night, but fat is bad because acquiring it and carrying it around raise the risk of death caused by predators. Wintering birds such as Great Tits face the Charybdis of a spiraling descent into overnight starvation and the Scylla of death in the sharp claws of a hungry, agile hawk.

The pallid term that modern behavioral ecologists invented to depict such a situation is "trade-off." A Great Tit faces a trade-off between starvation and predation risk. In the laboratory, where researchers can control the birds' access to food with electronically controlled doors on feeders, putting the birds on an unpredictable feeding schedule causes them to eat more and to gain weight. They perceive a starvation risk and so add fat. Putting the same, heavy birds back on a predictable feeding schedule causes them to eat less and to loose weight.[11] If there is no starvation risk, then it is better to shed the extra weight, to lower the risk of being caught by a predator. In nature, exposing the Great Tits to a model of a predator that slides over the feeder on a wire three times per day causes the birds to alter their daily schedule of feeding. Instead of gaining weight steadily over the course of the day, they delay feeding and then feed rapidly near the end of the day, thus lowering the number of daylight hours that they are out foraging and vulnerable.[12]

The Varying Value of a Male Child

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[11] Bednekoff, P.A. & Krebs, J. R. Great tit fat reserves: effects of changing and unpredictable feeding day length. *Functional Ecology* 9, 457-462.

[12] Macleod, R., Gosler, A. G. & W Cresswell, W. 2005. Diurnal mass gain strategies and perceived predation risk in the great tit *Parus major*. *Journal of Animal Ecology* 74, 956-964.

In the science fiction thrillers *Alien* and sequels, humans meet with arthropod-like creatures that insert an egg into the human. The egg develops inside the human and eventually a juvenile alien emerges, bursting through the human's abdominal wall. In the films, the aliens resemble arthropods, because the original writers, Dan O'Bannon and Ronald Shusett, almost certainly took the idea for a species that grows inside another species from real arthropods: the parasitoid wasps.

A parasitoid wasp lays her eggs on or inside the body of another insect larva or pupa, such as the caterpillar of a moth or butterfly or the maggot of a fly. The eggs hatch and the wasp larvae feed on the living body until they have grown sufficiently to pupate, emerging from the now consumed and dead host as new adults. There are thousands of parasitoid wasp species, each specialized for a narrow range of hosts. In agriculture, many parasitoid species are known as valuable controls of crop pests.

Typically, male wasps from a brood emerge first. The males usually have stunted wings and are incapable of flight. A male wasp waits for the emergence of females, mates with one or more of them (as long as there aren't too many other, competing males), and then dies. The newly mated females then fly away to search for a new host.

Because of this very specific life cycle, a female wasp that has found a fresh larva faces an unusual problem. If she is the only female to lay eggs on the host, all of her sons will compete with each other to mate. This is wasteful. The female could get more reproduction out of her brood if she could somehow produce mostly females, and just a few males to perform all the matings. In the wasps, this circumstance is probably what led to the evolution of a specialized mechanism of sex determination known as haplodiploidy.

The mechanism works as follows. When she mates, a female simply stores sperm in a compartment of her reproductive tract called the spermatheca. The sperm stored there can live indefinitely. The female then in effect decides whether to use the sperm when she lays each egg. As the egg passes down the oviduct, the female can release sperm from the spermatheca to fertilize the egg. A fertilized egg is diploid (two copies of each chromosome, one from the father, and one from the mother) and it will develop into a female. If the mother withholds sperm as the egg passes the spermatheca, the egg remains haploid (one copy of each chromosome from the mother only), but it still develops and it becomes a male. Haploid = male and diploid = female: haplodiploidy. Because of this method of sex determination, a parasitoid wasp female can control the sex ratio of the eggs that she lays on a host.

In nature, hosts may be scarce, or they may be concentrated in space (for example, fly maggots in a bird's nest). In either instance, more than one female wasp is likely to lay her eggs on the host. As the number of separate broods developing in a host increases, the value of a male offspring increases. Now, a male offspring can also mate with emerging females from other broods, and the males from other broods increase the level of competition. In 1967, the famous theoretical biologist William D. Hamilton referred to this situation as Local Competition for Mates,[13] and he predicted that the sex ratio of the brood

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[13] Hamilton, W. D. 1967. Extraordinary Sex Ratios. *Science* 156, 477-488

that a parasitoid wasp female lays should vary with the number of other females that have already placed broods in the host. The prediction is that when a female has the host larva to herself, she should produce about 20% sons, and that as the number of other broods in the host increases, the sex ratio that the female produces should converge on 50% sons.

Hamilton's prediction has been confirmed, in a number of species, in nature and in the laboratory, where the conditions that a female experiences when she lays her brood can be controlled. Females do lay more male eggs as the level of local competition for mates that her brood will meet with goes up. How do females "know" to do this? In other words, what are the stimuli that influence the sex ratio that a female produces? At least in one species, *Nasonia vitripennis,* a tiny wasp that lays eggs on fly pupae, we know that the presence of other females has an effect. When other females are nearby when a female lays her brood, she produces more males, but even more important is the presence of other eggs.[14] *Nasonia* females lay eggs on fly pupae. The pupa, a larval fly in the process of metamorphosing into an adult, is surrounded by a puparium, a tough shell. In her walking tour of a pupa after she finds it, a female wasp may detect the holes that other females drilled through the puparium. After she has drilled her own hole and inserted her long ovipositor to deposit eggs on the body of the pupa, she may be able to touch or smell other eggs. If she detects the eggs laid by other females, then she becomes less likely, as an egg passes toward her vagina, to contract the muscles that control the spermatheca, to allow

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[14] Shuker, D. M & West, S. A. 2004. Information constraints and the precision of adaptation: Sex ratio manipulation in wasps. *Proceedings of the National Academy of Sciences of the United states of America* 101, 10363–10367.

the egg to be fertilized. She lays more unfertilized, haploid eggs that will develop into males.

Infanticide Clock

I have written that natural selection acts to structure the brains of species so that individuals act as if they are constantly asking themselves the question, “what should I be doing at this moment to maximize my lifetime reproductive success?”. I will now make the first of two adjustments to that statement to improve its accuracy. In the quotation, I want to substitute “fitness” for “lifetime reproductive success.” What is the difference? Lifetime reproductive success is simply the number of offspring that an individual produces in its lifetime. Fitness is that number divided by the lifetime reproductive success of the most successful class of individuals in the population. In other words, fitness measures how much an individual reproduces compared to all other individuals in the population. Biologists want to measure fitness because it predicts the direction and rate of evolutionary change of traits. Fitness is what counts.

Because fitness is relative, an individual can increase its own fitness in two ways. First, it can reproduce more. Second, it can diminish the reproduction of others. Both ways increase an individual’s fitness. Thus, the effects of natural selection on individual traits are not to make individuals happy, or generous, or noble. It is to make individuals act to maximize fitness. This means that individuals often act in ways that, from the viewpoint of human societal norms, are brutally selfish and repugnant. An example of this is infanticide, infant killing by adult males. Infanticide is well documented in many animal species and it usually occurs in the same context: a male that is not the sire of an infant comes in close, often prolonged physical proximity to the mother and the infant.

Sarah Hrdy provided one of the first well documented cases from nature.[15] Hrdy studied langurs, a largish semi-terrestrial monkey in India. A langur social group comprises a dozen or so adult females and a single adult male, who chases all intruding adult males away and who evicts juvenile males as they start to mature. The group male has a temporary harem. It is temporary because the male typically will be able to keep his position for less than two years. Eventually, he is challenged and beaten by a male from one of the bachelor groups that form from evicted juvenile males.

The new male finds himself in a group with some females that carry infants. The father of these infants is the male that the new male just challenged and beat. Although the mothers work hard to protect their infants, the new male watches and waits for opportunities, and when he eventually gets his hands on an infant, he kills it. Infant killing by the new male carries a double fitness advantage for him. First he is diminishing the reproductive success of another male. Second, the mother, now without a suckling infant, will stop lactation and will cycle back into reproductive readiness soon. The sooner this new male can reproduce, the better, because his own fall from power is not that far away in the future.

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[15] Hrdy, S. B. 1977. *The Langurs of Abu: Female and Male Strategies of Reproduction*. Harvard University Press, Cambridge

Male infanticide tends to be found most often in species that have social structure like that of langurs: a single adult male has exclusive access to a group of females and this male is periodically deposed. However, male infanticide also occurs in species with more fluid social structures. It occurs in many rodents, including house mice. The house mouse is the most successful mammalian species. It has accompanied humans around the globe, and it is found on terrestrial habitats worldwide, including some very remote oceanic islands. It is a superb colonist, but it also can live at locally high densities. The species shows many finely tuned reproductive adaptations, including a rather spectacular control of infanticide.

In the laboratory, one can study the cues that influence infanticide by male mice. If researchers place a pink, hairless, blind day-old mouse pup in a cage with an adult male mouse they observe one of two reactions. The male may approach the pup, give an aggressive tail rattle, and then maul and bite the pup until it is dead. Or, the male may approach the pup, lick it, and huddle over it protectively. In most instances, we get the Mr. Hyde mouse. But, if researchers have recently provided the male with a female and he has copulated, we may get the Dr. Jekyll mouse. If the male copulates and then the researchers test him on successive days, an astoundingly clear pattern emerges.[16] On days zero to 17 after copulation, the response to a pup is infanticide. Then, at day 18 to 20 the male's response to a pup abruptly changes to parental and protective. Gestation in the house mouse is 18 days. Thus, copulation by a male starts a timer that goes off when a litter sired by that male could be born. When the timer goes off, infanticidal reactions to pups are inhibited for about a month.

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[16] Perrigo, G., Bryant, W. C. & vom Saal, F. S. 1990. A unique neural timing system prevents male mice from harming their own offspring. *Animal Behaviour* 39, 535-539.

Hot and Cold Lizards

In the vertebrate animals, there are two major energetic strategies, that we might call profligate and cheapskate. The profligate animals, known as the endotherms, are the birds and mammals. These animals use metabolic energy to maintain a high and constant body temperature. The production of all that heat requires very high rates of energy intake. High rates of energy intake are possible because the regulated body temperature allows animals to move actively for long periods of time in search of food. The endotherms are profligate: they have high rates of energy intake and high rates of energy expenditure. The cheapskates, called ectotherms, are the fish, amphibians, and reptiles. These animals do not use metabolic energy to regulate body temperature, and so their body temperatures fluctuate with the temperature of the surrounding environment. The energy requirements of these animals are much lower than those of endotherms, but they have a much more limited scope for activity, and their ability to move is affected by temperature. Most reptile species have a preferred body temperature, that they attempt to maintain by basking or by seeking shade. At that preferred temperature, an individual's ability to move is best; at higher and lower temperatures, ability to move is impaired.

Agama savignyi is a small, day-active lizard that lives mainly on desert sand dunes of the Middle East and adjacent parts of Africa. Because the species is relatively small, it has quite a few reptile, bird, and mammal predators, and because it inhabits sand dunes, it has a limited supply of shelters to duck into.

Researchers brought these lizards into the laboratory to measure the effects of body temperature on running speed.[17] They built a short racetrack with a rubberized floor for good traction, that was flanked by photocells linked to a computer. They then chased the lizard, by reaching toward it with a hand, to make it run down the racetrack. With this technique, they measured the maximum sprint speed that a lizard could reach when it was at different body temperatures. When the lizards were cold, at a body temperature of about 20 degrees C, they could run at a top speed of about 1 meter per second. Running speed increased with increasing body temperature up to the preferred body temperature of 35 degrees C, at which the lizards ran at about 3 meters per second. The researchers also discovered that the responses of lizards to the threatening hand varied with temperature. Warm lizards ran away almost immediately, but cold lizards did not. Although cold lizards could run slowly, their principal response to the researcher hand was to adopt a threatening posture, to gape, exposing the teeth, and to lunge and bite. The researchers reported that these bites were painful. *Agama savignyi*, a sand dune living lizard with limited sites to take shelter, modulates its responses to a threat based upon its own temperature and consequent ability to run well.

Peeking Ducks

Biologists still do not know what sleep is for, but we do know that most vertebrates and some invertebrates need to sleep. It is also clear that sleep poses a risk for any animal that

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[17] Hertz, P.E., Huey, R. B. & Nevo, E. 1982. Fight versus flight: body temperature influences defensive responses of lizards. *Animal Behaviour* 30, 676-679.

could be attacked. You can't watch for predators when your eyes are closed. In some birds, including mallards, the world's most widespread duck species, individuals ameliorate risk by occasionally opening an eye while they sleep. This brief eye opening, that David Lendrem[18] called "peeking," does not interrupt the characteristic brain wave activity of sleep, but it allows an animal to rouse from sleep if a threat is detected.

From a bridge over the Thames at Oxford, Lendrem watched mallards that slept on a wooden jetty that projected into the river. He watched individual birds for 2-minute sample intervals (paying attention to one individual at a time is called focal sampling), counted the number of peeks, and noted how far out the jetty the focal bird was. He found that a duck's distance from shore influenced the peeking rate (peeks per minute). The closer a duck was to shore and hence the greater its risk of attack by a ground predator such as a cat, the higher its peeking rate was.

Poker Face

A final example comes from my own observations of pronghorn, a native mammal of North America. Pronghorn resemble African antelopes but they do so only through convergent evolution. Pronghorn are the sole surviving species of a group of antelope-like creatures that lived in the North American grassland with a rich assemblage of other herbivores and carnivores. Pronghorn are famous for their running ability. They can sprint at almost 100 kph and they can also run for long distances at 60 kph. They can run fast and far because

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[18] Lendrem, D. W. 1983. Sleeping and vigilance in birds. I. Field observations of the mallard (*Anas platyrhynchos*). *Animal Behaviour* 31, 532-538.

until just 10,000 years ago, they were pursued by cheetahs, hyenas, lions, fast bears, and coursing dog-like species.[19] These predators and the other pronghorn species vanished in the end-Pleistocene extinction event. One predator that had a long coevolutionary history with pronghorn and that came through the extinctions with them was the coyote. Coyotes cannot catch an adult pronghorn but they are effective predators of pronghorn fawns. Pronghorn have been dealing with coyotes that hunt for their fawns for about 4 million years.

Like other hoofed mammals, pronghorn give birth to large, fast-growing young. The tactic here is to get the young big enough to outrun predators as soon as possible. A newborn pronghorn fawn weighs 4 kg and it gains about 0.25 kg per day. Despite this impressive size and growth rate (the mother's mass is only 45 kg) the fawn is highly vulnerable to a coyote for its first 3 weeks of life. Pronghorn, like most other hoofed mammals, have another strategy that is designed to protect young in the vulnerable weeks after birth. It is called the hiding strategy.

About an hour after birth, a pronghorn mother leads her tottering fawns (mothers always have twins) a few hundred meters away from the birth site, and then gives the fawns a signal to recline. The fawns walk away from the mother, choose a site, and sink out of sight in the ankle-high grass. The mother then moves away and stays away, giving a convincing impression that she is carefree, for about 3 hours. While she is away she sometimes walks close to the fawns, sometimes moves out of sight, over 400 meters away, but she maintains

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[19] Byers, J.A. 1997. *American Pronghorn. Social Adaptations and the Ghosts of Predators Past.* University of Chicago Press, Chicago.

an average distance of about 70 meters.[20] During this time, each fawn remains reclined and motionless, its chin resting on the ground. When she returns to the fawn, the mother allows it to consume a huge milk meal, and she licks the fawn's perineum to stimulate urination and defecation; she swallows the urine and feces. She then leads the fawn to a new location and signals it to recline. This cycle goes on for about three weeks.

The hiding strategy is all about denying information to a predator. First, the strategy withholds information about whether a fawn is present or not, and second, it provides only weak and useless information about the fawn's location. The average distance that mothers maintain from the hidden fawn makes it unprofitable for a coyote to simply search in a mother's vicinity. The amount of ground to be covered is too great. Coyotes do not engage in systematic search but in spring, when fawns are on the ground, coyotes do trot in short arcs toward solitary pronghorn females, observing them. When she is probed like this by a coyote, a pronghorn mother is perfectly deadpan. She simply stands, watching the coyote, until it moves away.

Now, the situation that I want to describe is as follows. Using a clock face to indicate positions, we put the mother at 12 o'clock and the hidden fawn at 6 o'clock. A coyote comes into view at 3 o'clock. The coyote is moving toward 9 o'clock. The coyote will pass directly between the mother and the hidden fawn. What does the mother do? She doesn't move. She stands and watches the coyote but she give no signs of alarm. She is denying the coyote any information about whether a fawn is nearby. In this situation, mothers have an

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[20] Byers, J. A. & Byers, K. Z. 1983. Do pronghorn mothers reveal the locations of their hidden fawns? *Behavioral Ecology and Sociobiology 13: 147-156.*

amazingly good poker face. What if the coyote appears at 3 o'clock and is moving toward 5, 6, or 7 o'clock? Now the mother's reaction is entirely different. She snorts, flares her big white rump patch, and prances in front of the coyote, running slowly enough to allow the coyote to close some of the distance to her. Running slowly, so that the coyote is right on her heels, she leads it far away. A pronghorn mother's reaction to a coyote depends entirely on the coyote's trajectory.

A Great Tit regulates how much it eats depending on its perceived risks of death by starvation and death by predation. A parasitoid wasp females alters the proportion of male eggs that she lays on a host depending on her perception of the number of competing broods that might be on the host. A male house mouse has a brain clock that tells him when it is OK to be nice to a mouse pup. Desert lizards change their responses to a threat depending on their own body temperature. When they sleep, Mallards scan the environment more when they are in riskier locations. Pronghorn mothers have completely different reactions to coyotes, depending on the coyote path of travel with respect to a hidden fawn. These are just a few examples of a general finding. Animals evolve the ability to adjust priorities, to modify their responses to a stimulus depending on context, when there is a fitness advantage to be had by doing so.

Chapter Four

Brains and Glands

Eating improperly prepared Fugu will kill you. You remain fully conscious while you become paralyzed and your breathing stops. Fugu refers to any of several species, commonly known as blowfish or pufferfish, that are found in Japanese cuisine. These fish are slow swimmers, propelling themselves only by movements of their fins. They compensate for the vulnerability that is created by slow swimming in two ways. First, they are able to inflate. They can quickly fill the stomach with enough water to swell into a spherical shape. This, combined with a spiny skin, makes then difficult or impossible to swallow. Second, these fish sequester in some organs and in the skin a poison that is produced by symbiotic bacteria that they have consumed. The poison, called Tetrodotoxin, or TTX (the fish belong to the Order Tetraodontiformes) is, gram for gram, about 100 times more lethal than cyanide. A lethal oral dose of TTX for an average-sized human is about 25 one-thousandths of a gram. Thus, in Japan, where the culture of eating these fish developed, the harvest, sale, and preparation of the food species is highly regulated.

Tetrodotoxin induces paralysis because it binds to and inactivates the Sodium channels in nerve and muscle cell membranes. These channels, which regulate the movement of Sodium across the cell membrane, are the basis for signaling in the nervous system and for the initiation of muscle contraction. The action of Sodium channels creates the two fundamental states of a nerve or muscle cell membrane: resting potential and action potential.

Potentials

A nerve cell, like any other cell, has an outer cell membrane, which is a double layer of fat. The double fat layer prevents atoms or molecules from simply diffusing into or out of the cell and so is the primary basis for the cell's ability to regulate traffic in or out. Embedded in the cell membrane are channels, proteins that are specialized to act as pores for specific atoms or molecules. Also embedded in the membrane are proteins that act as pumps, to move atoms across the cell membrane in one direction. A nerve cell has a cell body, from which a number of short branches, called dendrites, project, and from which a single long branch, called an axon, projects. Dendrites receive signals and the axon transmits signals. The axons of the nerve cells that control the muscles that move your eyes in their sockets are about 2 cm long. Those of the nerve cells that control a muscle in your big toe are 1.5-2.0 meters long.

Now, to arrange to make electrical recordings from a single axon (this was first done in squid, which have a giant axon, 0.5-1.0 mm in diameter, that drives the contraction of the mantle in the fast escape response), we set up two wires that are connected through a voltmeter. From the tip of each wire, we remove the insulation; this tip is called an electrode. Imagine the squid giant axon set up in a dish of seawater, into which we have introduced the electrodes. Now, we leave one electrode in the water and touch the other to the surface of the axon. Our voltmeter still reads zero. Now, we push the touching electrode through the cell membrane, into the interior of the axon. At the instant of penetration, our voltmeter registers a negative change: about -70 mV (mV = millivolt, or one-thousandth of a volt). The inside of the axon has a negative charge with respect to the outside. If we don't disturb our preparation, the voltmeter continues to read a steady -70 mV. This charge difference between the inside and the outside of the cell is called resting potential.

Resting potential comes about primarily through the electrochemical equilibrium of Potassium ions (K^+). Electrochemical equilibrium means that there are two effects, one electrical and one chemical, that control the local concentrations of a charged ion. The electrical effect is due to the attraction of opposite charges. Positively charged ions will move toward negative charges, and vice-versa. The chemical effect is diffusion. Ions such as Sodium (Na^+) or Potassium in a solution of water (the condition inside and outside of the cell) move until they are evenly distributed. If you drop a teaspoon of salt into a glass of water and simply wait, the Sodium and the Chloride ions will become evenly distributed; no part of the water will be saltier than another. Ions in solution move from an area of high concentration to areas of low concentration.

Inside the axon, there is quite a bit of negative charge that is created by protein molecules that have negative charges at several spots. These proteins are a permanent source of negative charge inside the axon. Embedded in the cell membrane are Na^+channels, K^+ channels, and a Sodium-Potassium pump. The pump works constantly, using stored energy in the cell to move Na^+ out of the axon and to move K^+ in. When the axon membrane is at resting potential, the Na^+channels are closed: no Na^+ ions can get through. Some of the K^+ channels are open. As a result of the pump and the channel settings, the concentration of Na^+ outside the axon is much higher than the concentration inside. The Na^+ outside cannot diffuse to the area of lower concentration because the Na^+channels are closed. The concentration of K^+ is higher inside than outside. Because some K^+ channels are open, K^+ can diffuse out of the axon. As each K^+ ion leaves, the balance between positive and negative charge inside the axon becomes more negative. Eventually, an equilibrium occurs where, for each K^+ ion that diffuses out, moving down a concentration gradient, another K^+ ion moves in, pulled by the negative charge. This electrochemical equilibrium results in a small negative change of about -70 mV inside the cell. This is called resting potential, but, as I have described, the cell is definitely not resting to maintain this potential. It is constantly running its Sodium/Potassium pump. The negative charge inside the axon is called resting potential because, unless it is disturbed, the axon membrane keeps this steady charge difference between inside and outside.

How, then, does an axon transmit a nerve signal, an action potential? The key to this event is the nature of the Na^+channels. These channels are sensitive to charge inside the cell. At resting potential, the channels are closed. When the cell becomes somewhat depolarized, moving from resting potential at -70 mV inside to about -50 mV inside, the Na^+channels begin to open. Remember that, due to the pump, the concentration of Na^+ outside the axon is much higher than the concentration inside. When the Na^+channels start to open, Na^+ diffuses into the axon. As Na^+ moves in, the negative charge inside the cell is erased, and this causes the Na^+channels to open further. The Na^+channels are described as voltage-gated. Because Na^+channels act this way, once the membrane reaches the point at which inward movement of Na^+ starts, there is no going back. The point at which Na^+ starts to move inward, at a membrane charge of about -50 mV inside, is called threshold depolarization. Once threshold depolarization is reached, the accelerating inrush of Na^+ is inevitable. There aren't many positive feedback mechanisms like this known in Biology. Most mechanisms are involved in maintaining a steady state and thus use negative feedback.

Now, let's stop for a moment at this instant. At this place along the axon, where threshold depolarization occurred, the axon has a positive charge (+50 to +100 mV) inside, because of all the Na^+ that rushed in. Immediately adjacent, the axon membrane is at resting potential: about -70 mV inside. The opposite charges so close to each other cause a flow of electric current that is sufficient to induce threshold depolarization, the inrush of Na^+, and the reversal of membrane polarity at the adjacent spot. This causes threshold depolarization at the next adjacent spot, and so on. This mechanism, like falling dominoes, is the way that action potentials are propagated along an axon.

Now we can go back to the instant at which the inward flow of Na^+ made the axon positively charged inside. At this instant, the Na^+channels begin to close due to a complex mechanism in the big protein molecule that is the channel. Also, K^+ is no longer held inside by negative charge, so K^+ diffuses out, restoring resting potential. The whole event - the inrush of Na^+ that reverses membrane polarity, and the outrush of K^+ that restores resting potential - occurs in about one-one-thousandth of a second. An action potential is a very brief flip-flopping of membrane polarity that propagates along the length of the axon.

How fast does the event travel? Speed depends on two things: axon diameter and myelin. Action potential velocity increases with axon diameter. So, when animal nervous systems are specialized to generate fast responses, the axons involved typically are huge, especially in the invertebrate animals, that don't have myelin. The squid giant axon, that directs the rapid contraction of the mantle, to jet the squid out of danger, is 0.50 - 1.0 mm in diameter. This size is truly huge for an axon, and the resulting conduction velocity is about 30 meters per second. Like squid, all the invertebrate animals use large diameter axons to achieve fast responses. The vertebrate animals acquired another, better, speed-enhancing trick: myelin. In vertebrates, most axons are wrapped with a fatty material called myelin, which leaves islands of unwrapped axon, the so-called Nodes of Ranvier, at regular intervals. This allows action potentials to jump from node to node, without propagating along the intervening myelinated section. This amazing trick allows even small diameter axons to conduct fast action potentials that reach speeds up to 120 meters per second.

Connections

I described the cell membrane phenomena that produce resting and action potentials in some detail to make a point about nervous system design and function. Because of the nature of action potential propagation, every action potential is the same, and the action potential at the end of the axon looks just like the action potential where it started. If all action potentials are identical to each other, how, you way be wondering, is any useful information transmitted within the nervous system? The answer, and this is the big point that I have been setting up, is that *all information is coded by the frequency of action* *potentials, the number per second that the nerve cell produces*. This is true for sensory neurons. A light versus a heavy touch, a soft versus a loud sound, a dim versus a bright light, a weak versus a strong smell - all of these differences are reported to the brain as differences in action potentials per second and in the duration of the volley of action potentials that travel along the axons of the sensory nerves. The same is true for interneurons, the nerve cells in the brain that send axons to other cells in the brain. The same is true for motor neurons, the nerve calls in the brain and spinal cord that send messages to muscles. All messages have the form of a volley of action potentials, and distinctions are made by the number of action potentials per second in the volley, and in the duration of the volley.

What are the effects of action potentials when they reach the target cell? Let's first consider motor neurons, the nerve cells whose axons project to a muscle. I wrote earlier that muscles are individually identifiable. We can name individual muscles, such as the biceps brachii, and describe the muscle's origin, its fixed point of attachment to a bone, and its insertion, its moveable point of attachment to a bone. Within this large, anatomically identifiable unit there are smaller functional units. A muscle is composed of many individual fascicles, and each fascicle contains a bundle of muscle fibers. Muscle fibers are huge long cells that develop from the fusion of many embryonic cells. Muscle fibers contain many fibrils, which are the highly organized protein filaments that can use stored energy in the cell to shorten. A motor nerve, as it nears its target within a muscle, typically branches several times to make contact with several muscle fibers. A motor neuron and the muscle fibers that it innervates collectively are called a motor unit. Motor units are the indivisible functional units of movement.

At the point where a branch of the axon comes into contact with the muscle fiber, the axon widens out into a plate-like structure that is separated from the muscle cell membrane by a tiny gap. This ending point is called a synapse. A synapse comprises a presynaptic membrane, where the axon ends, a synaptic cleft (the tiny gap), and a postsynaptic membrane on the receiving cell. When an action potential reaches the synapse, it triggers the opening of Calcium (Ca^{++}) channels in the presynaptic membrane. The inward movement of Ca^{++} sets off a chain of events that end when synaptic vesicles, small spherical storage bags inside the cell, move to the presynaptic membrane, fuse with it, and discharge their contents into the synaptic cleft. The compound that is released into the synaptic cleft is one of a class of compounds called neurotransmitters. At the neuromuscular synapse, the neurotransmitter is acetylcholine. Acetylcholine diffuses across the synaptic cleft and binds to receptor proteins that are embedded in the postsynaptic membrane. Binding induces the opening of Na^{+}channels and the initiation of an action potential that sweeps across the muscle cell membrane and then along membrane conduits deep into the fiber. In response to the action potential, the machinery of fibril shortening starts, and the muscle cell contracts.

A one-to-one relationship between an action potential arriving at the synapse and the muscle cell response is maintained by digestive proteins in the synaptic cleft that break down the bound acetylcholine rapidly. Rapid digestion means that if the muscle cell is to continue to contract, it must receive more action potentials. The digested components are taken up by the presynaptic membrane, re-synthesized to acetylcholine, and repackaged into vesicles. The enzyme that breaks down acetylcholine is called cholinesterase. Some of the most potent insecticides and human weapons of mass destruction (such as VX) are compounds that block cholinesterase.

Motor units vary in size. In small motor units, the motor neuron innervates just a few muscle cells. In large motor units, the neuron innervates a few hundred. When the muscle fibers of a small motor unit contract there may be no visible movement, even though there is a change in tension across a joint. When animals move, they typically activate small motor units first, and then recruit larger motor units only as needed. In addition, the force that muscle cells produce depends on the patterns of stimulation that they receive. If action potentials are closely spaced in time, the muscle cell smoothly increases the amount of force that it produces until it reaches a plateau of maximum force called tetanus. When motor neurons are active, they typically deliver sets of action potentials that are packed in time sufficiently to make the muscle cell advance toward tetanus, but with durations shorter than what would be needed to create tetanus.

Thus, there is a lot of very fine control of movement that is available to the nervous system. This is evident when we observe animals move gracefully in nature, witness an accomplished musical performance, read honesty or dishonesty in the facial expression of other humans, or listen to a song sparrow. Even the clumsiest human, when walking, is immensely graceful when compared to the most sophisticated modern robot.

Most of the neurons in the nervous system are not motor neurons. They do not deliver commands to muscles. Instead, they are involved in either reporting information from the sense organs (sensory neurons), or are involved in evaluation of the question, “what should I be doing at this moment to maximize my lifetime fitness?” (interneurons). The axons of sensory neurons or interneurons end on the cell body or a dendrite of another neuron. The point of ending is a synapse, much like the neuromuscular junction, and the effect of synaptic activity on the target cell is to make it either more likely to fire an action potential, or less likely to fire an action potential. The effect that makes a target cell more likely to fire an action potential is called excitation. The effect that makes the target cell less likely to fire an action potential is called inhibition. Each synapse involves the release of one kind of neurotransmitter (there are dozens of known neurotransmitters), and is either excitatory or inhibitory. At an excitatory synapse, binding of the neurotransmitter to the postsynaptic membrane causes Na^+ channels to open and that region of the target cell membrane to become depolarized. This is called an excitatory postsynaptic potential (EPSP). As in the neuromuscular synapse, enzymes in the synaptic cleft quickly digest bound neurotransmitter molecules to maintain a one-to-one relationship between input and effect. At an inhibitory synapse, binding of the neurotransmitter to the postsynaptic membrane causes chloride (Cl^-) channels to open, making the interior of the target cell at this point hyperpolarized, or more negative with respect to the outside. This is called an inhibitory postsynaptic potential (IPSP). Again, enzymes in the synaptic cleft quickly digest bound inhibitory neurotransmitter.

A neuron in the brain typically has hundreds to thousands of synapses on its cell body and dendrites. Some of the synapses are excitatory and some are inhibitory. An interneuron, then, is a tiny computer. It sums the EPSPs and IPSPs that spread across the cell membrane from moment to moment and, when average membrane polarity at the axon hillock, the synapse free part of the cell body just as it merges into the axon, reaches threshold depolarization, the cell fires an action potential. If excitation and inhibition are about equal, or if inhibition is predominant, the cell is silent, even though activity at its synapses may be prodigious. A neuron is a simple machine, making yes/no decisions from moment to moment based on the temporal and spatial sum of excitatory and inhibitory input. The rather daunting task for the discipline known as neuroscience is to explain how millions to billions of these yes/no machines can be linked together to produce perception, emotion, awareness, and the end product that these processes serve, adaptive behavior: animals that move smoothly through their environments, acting as if they were constantly asking themselves the question, "what should I be doing at this moment to maximize my lifetime fitness?".

The C-Start

One of the things that an animal must do to achieve fitness is to avoid being killed. If you're not alive, you can't reproduce. Picture a Great Blue Heron standing in a shallow stream. The bird is hunting. Its long, powerful neck is held cocked and at a shallow angle to the water, and its head is tilted slightly to one side. There is no motion at all. To fish below, the heron has become like a fallen tree branch in the stream. When the bird sees a fish swim into range, it strikes, plunging its beak into the water in a motion so fast that you can't see it. You only perceive that a movement has occurred. The heron's beak may emerge, holding a fish, but it may not. Failure to catch the fish does not occur because the bird's aim is poor. It occurs because fish can detect a heron's beak plunging through the water and can quickly jump to the side. The jumping motion is called a C-start and it also is blindingly fast[21].

High speed cinematography reveals that a C-start has two components. First, all the muscles on the side of the body opposite the heron's beak contract. This throws the fish's body into a C-shape, with the body wall rapidly bulging toward the heron's beak, pushing against the water and causing the fish to be propelled in the opposite direction. The fish then rapidly flips its tail, contracting the muscles on the other side of the body, to straighten out and scoot forward. The orientation of the fish's head after the initial part of the C-start is random in 180 degrees, so the direction of the animal's trajectory out of the C-start is unpredictable. How fast is blindingly fast? The fish perceives the wave energy created by the heron's beak in one part of its ear, where there are hair cells that are very sensitive to acceleration. Two one-hundredths of a second after the vibration reaches the fish's ear, the fish has attained maximal acceleration, at about 5 x g, away from the stimulus. That is indeed fast.

The C-start is orchestrated by two large cells, called Mauthner neurons, in the fish's hindbrain. The Mauthner neurons lie close to the ear on both sides of the brain, and their

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[21] Eaton, R.C., Bombardieri, R.A. & Meyer, D.L. 1977. The Mauthner-initiated startle response in teleost fish. Journal of Experimental Biology 66, 65-81.

huge axons cross the midline and descend in the spinal cord to make synapses with motor neurons on that side. Activity by the left Mauthner neuron causes all the muscles on the right side of the body to contract, and vice-versa.

Axons from the ear hair cells branch to make two connections. The first is to excite interneurons that inhibit the Mauthner cell. These interneurons send axons to synapses on the Mauthner cell and their activity creates IPSPs. This kind of nervous system design is called feed-forward inhibition. The second branch of the hair cell axons forms excitatory synapses directly on the Mauthner call. Thus, at most times, when the fish's ear is detecting the kinds of vibration that are associated with water currents, a twig dropping into the stream, the fish's own movement, the movement of other fishes nearby, the IPSPs created by feedforward inhibition outweigh the EPSPs and the Mauthner cell is silent. However, the rapid acceleration caused by the heron's plunging beak causes prolonged rapid volleys of action potentials from the ear hair cells and now the EPSPs outweigh the feedforward IPSPs, and the Mauthner cell fires an action potential.

Here we have a very clear explication of the neural basis of a sign stimulus. Recall from Chapter One that the ethologists, by keen observation and simple experimentation, had shown that behavioral responses are often elicited by specific components of an overall stimulus. A heron's beak plunging toward a fish has a particular size, shape, color, and characteristics of movement, but all of these are irrelevant to the fish. The fish's nervous system is designed to detect that part of the heron's strike that is the most reliable indicator that a strike is indeed happening. In this case, that part is the vibration created by the plunging beak. That vibration discriminates between a heron strike and all other events in the fish's life. Thus, because the fish has a good discriminator, it pays attention to the vibration and ignores the other components of the stimulus. The elements of nervous systems that are set up to make discriminations of this type are called feature detectors. The truly amazing perception of the ethologists was that, with the concept of sign stimuli, they implied the existence of feature detectors before neuroscientists had described them.

The huge axon from a Mauthner cell excites motor neurons in the spinal cord on the opposite side of the body, but the axon also sends branches to interneurons that inhibit the motor neurons on the same side as the active Mauthner neuron. Neuroscientists now have evidence that the huge diameter of the Mauthner axon, which makes action potentials travel very fast, mainly exists to ensure that inhibitory commands to the side that should remain relaxed always arrive before any other sources of excitation[22]. Another early branch of the Mauthner axon crosses to the other side of the brain and excites interneurons that inhibit the other Mauthner cell. Finally, another early branch excites interneurons that inhibit the active Mauthner cell. This design, in which a neuron turns itself off, is called recurrent inhibition.

To recapitulate, the fish's ear detect vibrations caused by the heron's predatory strike. Action potentials from the ear hair cells excite and inhibit the Mauthner cell on that side, but the sum of excitation is greater, and the Mauthner cell fires an action potential. Branches of the Mauthner axon result in inhibition of the contralateral Mauthner cell,

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[22] Eaton, R.C., Hofve, J.C. & Fetcho, J.R. 1995. Beating the competition: the reliability hypothesis for Mauthner axon size. Brain, Behavior and Evolution 45, 183-194.

inhibition of the active Mauthner cell after the action potential has left, massive excitation of contralateral muscles, and equally strong inhibition of muscles on the side of the predatory strike. This arrangement of excitatory and especially of inhibitory effects ensures that when the heron strikes, only one Mauthner cell will fire, and only the muscles on the opposite side of the body will contract. Because there are very few synaptic connections between the ear hair cells and the trunk muscles, and because the Mauthner axon is huge, the response is very quick.

The Mauthner initiated C-start represents an instance in which we understand in complete detail how an animal evaluates the question, “what should I be doing at this moment to maximize my lifetime fitness?”. The adaptive response to the heron’s strike comes about by ignoring a lot of sensory information, by the arrangement of feedforward inhibition and excitation of Mauthner cells that creates a feature detector for sudden vibration, by contralateral and recurrent Mauthner cell inhibition, by fast traveling preemptive inhibition of muscles on the side of the strike, and, finally, by excitation of the contralateral muscles.

The same design principles underly all animal behavior, and ultimately, we will understand the mechanistic basis for all decision making. The fly’s decision to inflate her proboscis to dab at sugar on your table, your decision to rise and reach for the fly swatter, the fly’s decision to jump and fly as your lethal strike started: all come about by nervous system design that is fundamentally the same as the mechanism that causes the C-start. The main difference between the fish's decision and your decision lies in the number of interneurons that intervene between sensory input and motor output.

Crab Chewing

For obvious reasons, the Mauthner cells are referred to as command neurons. They exert complete, top-down control of a motor act. Although there are other examples of command neurons, there aren't many. Typically, as I implied above, motor output comes about as the result of interactions among several to thousands of interneurons. To study the ways that neurons interact to create motor output, a good place to start is with small networks of neurons that produce highly regular, patterned motor output: central pattern generators (CPG)[23]. CPG are responsible for rhythmic motor acts such as breathing, chewing, and walking, and they produce their motor commands on their own, without need for timing messages from sensory neurons or other interneurons. CPG even continue to produce their characteristic output when removed from the animal and placed in a dish, so they are amenable to many kinds of experimental investigation.

Two CPG that became an intense subject for neuroscientists are those that direct the contraction of muscles in the stomachs of crabs and lobsters. These CPG lie in the somatogastric ganglion, a small cluster of neurons inside a blood vessel where it passes across the top of the stomach. The gastric mill CPG creates the chewing movements of the fore-stomach, in which three hardened plates in the stomach wall are brought together to

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[23] Selverston, A.I. 2010. Invertebrate central pattern generator circuits. Philosophical Transactions of the Royal Society B 365, 2329-2345.

cut and grind food. In the lobster, the gastric mill CPG contains 11 neurons, 10 of which are motor neurons and one an interneuron. The pyloric CPG contains 14 motor neurons that generate the peristalsis-like movements of the second chamber of the stomach. In both CPG, the motor neurons send excitation to the muscles that they innervate, and send inhibition to the other neurons in the CPG. The CPG neurons also fire spontaneous action potentials (due to specialized leaky Na^+ channels) at different rates. Rhythmic chewing and peristalsis-like movements come about as emergent properties of small networks of spontaneously active, mutually inhibitory neurons. Neuroscientists have studied the crustacean somatogastric ganglion for over 30 years, and now know the complete wiring diagram of each CPG and know a lot about the individual membrane characteristics (density and types of ion channels) of each neuron. Thus, we now have a clear understanding of how a crab manages to chew its food.

One of the surprises that emerged from this work was the discovery that a simple network of motor neurons can produce more than one pattern of neural output. For example, the gastric mill CPG can cause the three stomach teeth to come together in two distinct ways. Varied output from a simple network occurs because of another important cellular event called modulation[24]. Besides ion channels, nerve cell membranes have proteins embedded in them that bind with modulatory compounds that are delivered by other neurons. Modulators are neurotransmitter-like molecules. When they bind to the receptor proteins in the target cell membrane, they induce a cascade of cellular events inside the target neuron that alters the functional characteristic of neuron’s ion channels. This causes the

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[24] Harris-Warrick, R.M. & Marder, E. 1991. Modulation of neural networks for behavior. Annual Review of Neuroscience 14: 39-57.

neuron to respond differently to the inputs from other neurons. Modulation alters the firing characteristics of individual cells, allowing a simple network of neurons to produce multiple, distinct outputs. In crabs and lobsters, there are over 20 neuromodulators that affect the operation of the somatogastric ganglion. These come from neurons outside the ganglion and from the neurons that make up the CPGs.

The significance of the decades of work on the crustacean somatogastric ganglion was not that it allowed us to understand exactly how crabs manage to chew, but rather that it portrayed the design features of a network of neurons. Crab chewing is thus a portal into the understanding of all perception, thought, and motion.

Reward

Another class of chemical compounds that have modulating effects on neurons in the brain are the hormones. Hormones are small molecules, produced by the endocrine glands, that enter circulation and travel throughout the body. The targets of any specific hormone are designated by receptor proteins, embedded in cell membranes, that bind to the hormone. Many neurons in the brain have hormone receptors and the binding of hormones to these receptors causes often profound shifts in behavioral priorities. As we saw in the previous chapter, animals evolve the ability to adjust their responses to stimuli when environmental contingencies make it adaptive to do so. One of the main mechanisms by which the adjustment of behavioral priorities occurs is by the modulating effects of hormones.

Consider a seasonally breeding temperate mammal such as the North American elk. Female elk will come into estrus (behavioral and physiological readiness to mate) in September, so males must be ready to mate and to compete for mating opportunities then. Male achieve readiness with hormonal switching. After the summer solstice, shortening day length initiates signaling in the male elk brain that causes the hypothalamus, a basic control center just above the roof of the mouth, to release a hormone called Gonadotropin Releasing Hormone (GnRH). GnRH is transported by a specialized venous portal system to the anterior pituitary gland, located just below the hypothalamus. In response to GnRH, cells in the anterior pituitary release another hormone, Luteinizing Hormone (LH) into circulation. LH binds to receptors on cells in the elk's testes and causes these cells to synthesize and release the hormone testosterone. Testosterone in circulation has widespread effects. It induces the testes to grow and to produce sperm. It induces general muscle growth and especially growth of the neck muscles. It partially suppresses the immune system so that the male will have more energy available for mating competition. It causes the skin that covered and nourished the male's antlers while they grew to dry and shred off. It binds to receptors on neurons in the brain, inducing multiple changes in the male's behavior. Now the male begins to scent mark with urine, spraying it on his chest and in mud pits where he will wallow. The male begins to sing, emitting the squealing blasts called bugles. He begins to try to monopolize access to groups of females, and becomes willing to fight with other males to maintain his monopoly. He becomes sensitive to the compounds in female urine that indicate the approach of estrus, and when he detects a female nearing estrus, he performs the actions that constitute courtship in elk. Finally, if successful in all the above, he copulates with females that accept him.

In this and in many other instances, hormones orchestrate integrated physiological and behavioral changes that allow animals to respond appropriately to their surroundings. For the most part, control operates as I have described for testosterone. Neural signals integrated in the hypothalamus cause neurons to secrete releasing hormones that are transported to the pituitary gland, where they induce or inhibit release of a pituitary hormone. The pituitary hormone enters circulation, binds to receptors on cells in the target endocrine gland, and induces the gland to release a hormone. As illustrated in the elk example, many hormonal effects on behavior have to do with preparing an animal to mate or to care for young. Hormones create the brain changes that induce a mother to form a bond to her young and they influence the formation of social bonds between mates in monogamous species. Hormone effects on the activity of the neurons to which they bind create what we subjectively experience as love.

Because hormones can have such large effects on behavior, one way in which rapid evolutionary change in behavior can occur is by a change in the density of hormone receptors in the brain. This kind of change apparently was the basis for the evolutionary switch to monogamy in a small rodent called the prairie vole. There are many species of voles (also called field mice), and most are decidedly not monogamous. In most vole species, males seek out receptive females, mate with them if permitted, and then resume patrolling for other receptive females. In contrast, when a young prairie vole male finds an unmated female, the two copulate repeatedly and as a result they form a social bond. Their copulation genuinely is “making love.” As a result of the bond, the male remains close to the female, guards her and the vicinity of the nest, and helps to care for the pups when they are born. This switch to monogamy in the prairie vole is in part due to a single mutation that results in a greater level of expression of the gene that makes the receptor for arginine vasopressin, a hormone made in the hypothalamus[25]. A comparison of the brains of prairie voles to the brains of other species of vole shows, in prairie voles, a much greater density of arginine vasopressin receptors in the brain areas that are associated with reward.

"What's this?" you say. There is a brain area that creates reward? There most certainly is, and activity in the reward circuits is involved in learning, in getting an animal to repeat behavior that is reliably associated with outcomes that lead to an increase in fitness. The addictive drugs in humans are those that activate the reward circuits. The existence of the reward system is powerful confirmation of our assumption that brains should be structured so that animals act as if they are constantly asking themselves the question: "what should I be doing at this moment to maximize my lifetime fitness?" The reward in effect tells animals that, when they eat, maintain a healthy body, and especially when they mate, that what they are doing is contributing to fitness. If a rat has an electrode placed into one of the reward areas of its brain and then is given the opportunity to deliver electrical stimulation to that area by pressing a bar, the rat does much bar pressing. It becomes a bar press junkie, lying on its side so that its wrist is optimally poised over the bar to press at 100 times per minute for hours at a time, even when this means losing the opportunity to eat or drink.

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[25] Lim, M.M. & Young, L.J. 2004. Vasopressin-dependent neural circuits underlying pair bond formation in the monogamous prairie vole. Neuroscience 125, 35-45.

Brain Stimulation

Electrical stimulation of brains has uses other than producing bar-pressing obsessed rats. Stimulation allows us to map function, to show where in the brain specific tasks are performed. Paradoxically, humans make good subjects for this kind of work. Although the human brain is the largest animal brain and the most complex object in the known universe, brain stimulation is performed while subjects are awake and so subjects can orally report what they experience when stimulation occurs. Brain stimulation of humans is done in the context of surgery for epilepsy or brain tumors, to identify the areas that should be spared when the goal is to remove some amount of brain tissue. This kind of work has been done for about 100 years[26].

Stimulation can induce basic physiological events such as blushing, nausea, changes in heart rate or breathing rate, changes in blood pressure, and sweating. Stimulation can induce emotional states such as anxiety, fear, anger, sadness, and mirth. Stimulation can induce motor output such as speech, changes in facial expression, eye movement, movement of limbs, and laughing or crying without feelings of happiness or sadness. Stimulation can induce the urge to move or the sensation that movement has occurred, visual, auditory, taste, and smell hallucinations, the recall of memories, the sensation of leaving the body, déjà vu, and impairments in reading, naming or speaking.

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[26] Selimbeyoglu, A. & Parvizi, J. Electrical stimulation of the human brain: perceptual and behavioral phenomena reported in the old and new literature. Frontiers in Human Neuroscience 4,1-11.

These studies are useful in that they show where emotions, sensations, and movements are generated, but they don't take us very far into the understanding of the actual neural mechanisms that are involved. A bit more understanding is made possible by stimulation experiments on animals. The animals can't report what they are feeling, but it is possible to study how motor output is produced in a more controlled, systematic way that is ethically permitted in humans. Recent work on monkeys has shown that there are areas of the so-called pre-motor cortex where motion goals seem to be encoded[27]. For example, stimulation in one area results in a monkey bringing its hand to the center of its chest, irrespective of the initial position of the hand. If the hand is below the chest, one set of muscles must be contracted, but if the hand is above the chest, another set is involved. So the "intent" center works through an output area that incorporates feedback from the current position of the limb.

Nevertheless, there is a somewhat frustrating disconnect between the studies like those of the crustacean somatogastric ganglion, where we understand in almost complete detail how a network of neurons produces motor output, and studies of movement that is produced by the brains of flies, monkeys, or humans. I wrote that studies like those of the somatogastric ganglion are the portal into the understanding of more complex output of nervous systems, and it seems that most neuroscientists would agree. However, there is still a long way to go. As Michael Dickinson[28] put it, " Fortunately, many challenging

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[27] Graziano, M. 2006. The organization of behavioral repertoire in motor cortex. Annual Review of Neuroscience 29, 105-134.

[28] Dickinson, M. 2006. Insect flight. Current Biology 16, R309-R314.

problems remain, otherwise, engineers and toy makers would have already littered the world with tiny mechanical flies.”

Chapter Five

Instinct

If you step outside on a summer morning almost anywhere in the world, you hear bird song. If you live in a natural or even a semi-natural area, what you hear is better described as a cacophony. You don't even have to step outside. The bird song of several species that started at first light probably awakened you as it came through the open window. Bird song is loud and it is repetitive.

For the most part, it is the male birds doing the singing. Each male has claimed an area of space from which he will attempt to exclude all other birds except his mate. This is his territory. The territory contains the site where the male and his mate build their nest, and it often contains enough surrounding real estate to provide the food that the male, his mate, and their brood will need. By defending a territory, a male can ensure that the resources that he needs to reproduce are available, and close at hand. Territoriality is very common in animals. It has evolved independently many times because, quite often, the cost of defending a territory (offspring equivalents of the time, energy and risk spent in patrolling and defending borders) is less than the benefit (additional offspring produced as a consequence of owning the defended resources).[29]

Male birds defend their territories by patrolling the boundaries, threatening and chasing away intruders, and occasionally by entering into knockdown, drag-out, fall-to-the-ground-

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[29] Brown, J.L. 1964. The evolution of diversity in avian territorial systems. *Wilson Bulletin*, **76**, 160-169

and-pummel-your-opponent fights. But patrolling, chasing, and fighting are costly activities. Although territoriality will persist, evolutionarily, as long as the overall cost is less than the benefit, the individuals that are able to shrink cost even more will have that many more resources to put into offspring, and hence higher fitness. One way that a male bird can reduce the cost of territorial defense is to advertise that the territory is occupied. He can sing. Song is a relatively cheap way for a male to broadcast the message, "This space is taken and if you cross the line I am going to punch your lights out." To be effective, the message must indeed be broadcast. This is why bird song is so loud and so repetitive.

Bird song is loud and repetitive, but it also seems quite difficult to produce. The difficulty in production is not immediately easy to understand. It seems reasonable to think that a bird could advertise his presence on a territory perfectly well with the vocal equivalent of a Vuvuzela - a loud, single note. This is not what birds do. Instead, they produce loud, multi-note complex sounds that genuinely qualify as song. The sounds that they produce usually represent virtuoso performances that far exceed the abilities of any human vocal performer.

Figure 5.1 shows a sonogram of one of the songs of a song sparrow male. A sonogram is a way of visually representing a sound. Time is represented on the X axis, and sound frequency is represented on the Y axis. Amplitude at any time and frequency is represented by the amount of black. In the 1940s, before this technology existed, Donald Griffin struggled with ways to visualize and measure the echolocating clicks of bats. Now, anyone can with ease download and use the software that makes these visual representations of sound.

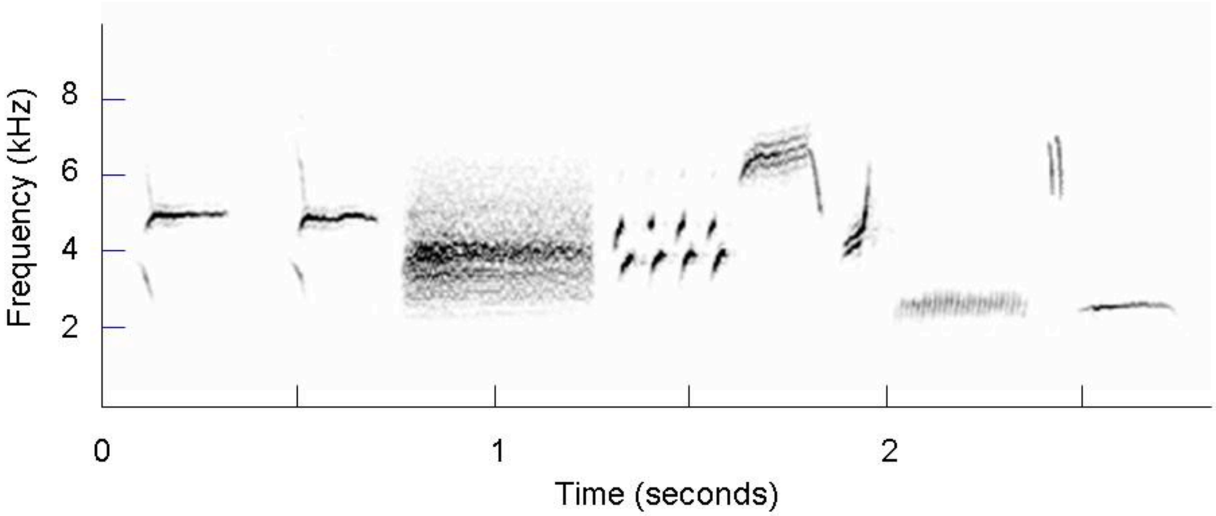

Figure 5.1 - A sonogram of one song type produced by a song sparrow male. The sound recording and figure production were made by Mike Beecher, who has studied the song of these birds in Discovery Park, Seattle, Washington, for many years.

Listening to the two-second song depicted in Figure 5.1, you would hear two distinct introductory notes, a breathy buzz, four punched, staccato notes, a high tone followed by a grace note to a low buzz, another high grace note before a low whistle. At normal speed, the inexperienced listener would find it difficult to discern these distinct song elements because they are packed together so closely. The human listener also would not hear the steep frequency sweeps (a vocalist would recognize these as impossible glissandos) in the introductory notes and in the high tone and grace note that follow the staccato passage. Finally, notice in the two introductory notes, that while the bird is producing the loud clear tones that start with a short upward frequency sweep, it is simultaneously producing a lower note that is a downward frequency sweep! Birds are capable of vocal feats like this because the syrinx, where sound is produced, has vibrating membranes on right and left sides that have separate muscular control and innervation.

Why bird song embodies such striking virtuosity is not known, but the question is under investigation by quite a few labs. One hypothesis is that the song not only reveals that the territory is occupied, but also broadcasts some advertisement about the skill, health, and vigor of the singer. If a male can produce a proficient, highly technical motor performance, perhaps he is not to be trifled with. Another hypothesis is that an important intended recipient of song is the female that may become or has become the male's mate. With skilled motor performance, the male may be trying to convince the female that he is a worthy sire for her offspring[30].

Whatever the evolutionary history and current function(s) of bird song, we know that song is highly complex, skilled motor performance that must involve precise control of the muscles that control breathing, the syrinx, the throat, the trachea, and the beak. What I want to discuss in the context of this chapter is the extent to which bird song is an instinct.

How does that Song Go?

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[30] Byers, J., Hebets, E. & Podos, J. 2010. Female mate choice based upon male motor performance. *Animal Behaviour* 79, 771-778.

Peter Marler, who provided a key conceptual entry into our understanding of bird song, began to study white-crowned sparrows in the bay area of San Francisco starting in 1957, when he took a faculty position at Berkeley. Extending work that he had done on some European birds for his doctorate at Cambridge, Marler sought to explain the existence of local song dialects in the sparrows. Local song dialect means that if we cross the Golden Gate Bridge and record the song of white-crowned sparrows in Marin County, we detect song that, although species-typical, sounds consistently a bit different from the song that we recorded in Palo Alto. And, the birds in Berkeley also have another, distinct dialect. Over relatively short distances for animals that are as mobile as birds, there is local, slight, but discrete differentiation of song. Marler's approach to figuring out why dialects persisted involved describing how song appeared to develop in nature, and then conducting a series of laboratory experiments, to intervene at different points in that development[31].

In nature, what we observe is that a white-crowned sparrow male hatches, and is fed by his parents until he fledges (is able to fly away from the nest). During this time, he frequently hears his father singing, but he himself is silent, except for the begging calls that he emits to elicit parental feeding. Sometime well after fledging, at about 150 days of age, the young male begins to sing. His songs at first are rudimentary, rather poor copies of white-crowned sparrow song, but he continues to sing, and over the next 50 days, his song improves until it sounds just like Dad's. This period of practice and improvement is called subsong, or plastic song.

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[31] Marler, P. 1970. A comparative approach to vocal learning: song development in white-crowned sparrows. *Journal of Comparative and Physiological Psychology* Monograph 71, 1-25.

Marler's experimental approach was to take newly hatched nestlings from nature and to raise them in a laboratory setting where he could record all sounds that the birds produced and could control the sounds to which they were exposed. An extensive series of experiments established several facts about the way that song develops in white-crowned sparrows. For example, if birds are taken from the nest in the first week after hatching and raised in auditory isolation, they enter subsong at the appropriate age, but the song does not improve to the adult type. Marler obtained the same results when the young birds were exposed only to the songs of another species, the song sparrow. In other words, if a young white-crowned sparrow hears only the songs of another species, it is as if he has heard nothing. Further experiments showed that, to develop normal song, the young male must hear white-crowned sparrow song sometime between 10 and 50 days after hatching. This is an example of what is called a sensitive period. There is a range of ages during which the brain may be modified by experience. If the necessary experience falls outside the sensitive period, the brain modification does not occur.

The young bird is on track to develop normally if it hears white-crowned sparrow song during the sensitive period for song learning. Then, about 100 days later, the bird enters subsong. Marler hypothesized that, during subsong, the bird must be comparing the sounds that it produces to the songs that it memorized during the sensitive period, trying for a better and better match. To test this hypothesis, Marler deafened birds before they started subsong. The results were as predicted. Birds that could not hear themselves did not improve. Birds must be able to hear themselves singing during subsong to alter the motor program to that of adult song. Marler also deafened birds after song development was complete, and showed that song was unaffected. White-crowned sparrow males must be able to hear themselves while they are in the self-tutoring phase of subsong, but after that, the motor program is set in its final form (Marler's term for this was "crystalized"), and sensory feedback is irrelevant.

To recapitulate, a white-crowned sparrow male hatches. From its nest, it hears its father singing, the songs of neighboring white-crowned sparrow males, the songs of other bird species, cricket chirping, frogs calling, perhaps automobile horns and human voices. The bird has an instinctive feature detector that allows it to recognize white-crowned sparrow song. When the feature detector is activated, a memorization program starts, and the young bird stores a detailed accurate copy of adult song. Three to four months later, the bird starts to sing, and it compares the songs that it produces to the memorized song, modifying motor output until there is a perfect match. Marler had found the explanation for song dialects. Local dialects exist because of the memorization-based mechanism by which song develops.

What Marler had discovered was a program of behavioral development that is nearly ubiquitous in songbirds and is now referred to as sensorimotor song development. In songbirds, the basic arrangement of a memorization phase that is followed somewhat later by a practice phase is the norm, but there is substantial variation in several aspects of the learning program[32]. The duration of the sensitive period for memorization varies from a

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[32] Beecher, M.D. 2010. Birdsong and vocal learning during development. *Encyclopedia of Behavioral Neuroscience* 1, 164-168.

fairly narrow window (as is true for white-crowned sparrows), to the first entire year of life, to lifetime ability to learn. Some researchers categorize bird species as either closed-ended or open-ended learners. At the extreme open end are bird species such as mockingbirds or starlings, that are called mimics. Seemingly throughout life, individuals of these species are able to memorize and then produce accurate copies of sounds. A starling living with humans repeated the question, "Does Hammacher Schlemmer have a toll-free number?" on the day after hearing a human say it once[33]. Among non-mimetic species, there is still quite a bit of variation in how many songs are learned, how accurately the memorized songs are copied, and the stringency of the feature detector that turns on song-memorization.

Instinctive ***and*** *Learned*

Now, to come back to the topic of this chapter, is song in white-crowned sparrows instinctive, or is it learned? Is it nature or nurture? Obviously, it is purely neither. It is both. Bird song is not completely instinctive, because the young bird must learn by memorization exactly how its songs should sound, and must learn to produce these sounds by practicing. Bird song is not completely learned, because the bird has a feature detector that identifies what it should memorize, and it has a pre-set developmental schedule that determines when the sensitive period for learning will open, when it will close, and when the period of subsong will start. Bird song develops through an interaction between instinctive and learned components. It is a form of programmed learning. When we

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[33] West, M. J. & King, A.P. 1990. Mozart's Starling. *American Scientist* 78, 106-114.

understand how song develops, to ask whether song is instinctive or learned begins to seem irrelevant, even silly.

The evolutionary biologist Ernst Mayr offered a better way to think about the development of any motor act[34]. Mayr noted that, instead of a dichotomy (nature-nurture), there was a continuum between what he called closed and open motor programs. The development of every behavioral act falls somewhere on the closed-open continuum. At the closed end are motor acts that do not develop; the motor pattern exists in its complete form when the animal is born, and the elicitation of the motor act is controlled by feature detectors. Behavior at this end of the continuum is often what ethologists offered to illustrate the concept of instinct. For example, a nest parasitic cuckoo chick immediately after hatching pushes other eggs and chicks out of the nest. A red kangaroo, like all marsupials, is born as a tiny embryo. The embryo must travel from where it emerges, the opening of the vagina, upward to the mother's pouch, where it will find a nipple and complete the remainder of development nourished by milk. When a red kangaroo is born, its hind limbs are rudimentary stumps but its front limbs are functional and quite muscular. The embryo swings its trunk to the left to advance the right forefoot, then swings the trunk to the right to advance the left forefoot, thrashing from side to side like a salamander to move upward to the lip of the pouch. The mother does not assist. The embryo must make this epic trek on its own, so the trashing motor program must be ready to go at the moment of birth. A human infant, like all mammal infants, when touched on the lips by the mother's nipple,

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[34] Mayr, E. 1974. Behavior programs and evolutionary strategies. *American Scientist* 62, 650-659.

opens the mouth, closes the lips around the nipple, and turns on a complex motor program called sucking.

Most animals (corals, jellyfish, flatworms, nematode worms, earthworms and their marine relatives, clams, crabs, shrimp, spiders, insects: that's over 99%) have small, economical nervous systems and relatively limited ethograms, in which acts are mostly on the closed end of Mayr's continuum. However, even in animals with tiny brains, we may find instances in which a motor act is modified by experience. The water stick insect *Ranatra linearis* is a true bug that lives on the surface of fresh water, resting on twigs or leaves with its head usually underwater to detect prey such as tadpoles. When the insect sees a tadpole swim within range, it strikes with immensely long forelegs that are two-thirds the length of the body. If the insect is to strike effectively, it must somehow be able to calibrate the input from the eyes to know when a tadpole is within range of the forelegs. Life is further complicated for this predator because, like all insects, it grows by periodic molts, jumping from one fixed size to another. Size jumps are a consequence of having a hard inflexible external skeleton. To grow, the insect must reabsorb most of the old cuticle, swell with air or water to spilt the old cuticle, crawl out of it, and then harden the new underlying cuticle while it is still swollen and oversized. After the new cuticle hardens, the insect has some new room to grow into, like a child whose parents buy it shoes a size or two too large. When *Ranatra* molts, its forelegs change in size and it acquires new ommatidia in the eyes. The new ommatidia appear centrally and push existing ommatidia to the periphery. To register these changes in the brain, *Ranatra*, in the first 3-4 hours after a molt, executes many slow motion flexions and extensions of the forelegs and openings and closing of the claws. These practice movements are required to recalibrate the input from the eyes and output in the form of motor commands to the leg muscles[35]

Figure 5.2 - *Ranatra linearis*

Modification of the predatory strike in water stick insects is an example of a motor program that is just slightly off the closed end of Mayr's continuum. A bit further along the continuum is behavior such as bird song, with its programmed memorization and practice. Still further out the continuum is locomotion in the fancy movers, the birds and mammals, in which basic locomotion is run by central pattern generators, but in which fine control of movement develops through extensive, performance-based learning. In birds and mammals, the cerebellum, a part of the brain where fine tuning of motor commands occurs, is very large. In mammals and probably also in birds, there is a postnatal sensitive period during which performance-based loss or retention of synapses in the cerebellum occurs. There is an initial overproduction of synapses: more synapses are formed than will be retained into adult life. Then, during the sensitive period, the synapses that are active

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[35] Cloarec, A. 1982. Predatory success in the water stick insect: the role of visual and mechanical stimulations after molting. *Animal Behaviour* 30, 549-556.

during a movement are retained, and the synapses that are not active tend to be lost. In mammals, this sensitive period coincides with the ages during which young individuals express the goofy looking, extravagant leaps, twists, cavorting, running, and mock flighting that we call play[36]. Also somewhere in the same neighborhood of the continuum is human speech, which has some lifelong learned components, but which also shows striking similarity in its development to bird song. Similarities in the developmental programs were first noted by Peter Marler[37]. Like bird song, human speech development involves an initial memorization period aided by feature detectors that instruct the infant what to memorize. Also like bird song, there is a sensorimotor phase, called babbling, in which the infant appears to compare the sounds it produces to what it has memorized. During babbling, speech does not improve if the infant cannot hear. Finally, like bird song, human speech appears to have specific sensitive periods. The human languages share many phonemes (the individual motor acts of speech) but not all. If a child is not exposed to a phoneme before puberty it will not be able to hear the phoneme as distinct from others, and will not be able to produce it correctly. Thus, immigrants, if they arrive before puberty, generally end up sounding like native speakers, but those arriving after puberty always have a distinct foreign accent. Richard Dawkins tells a story about delivering an address in Japan. At the end of his talk, his host stood and said, "Thank you Dr. Dawkins, we will now crap for you."

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[36] Byers, J.A. & Walker, C.B. 1995. Refining the motor training hypothesis for the evolution of play. *The American Naturalist* 146, 25-40.

[37] Marler P. 1970. Birdsong and speech development: Could there be parallels? *American Scientist* 58:669–673.

To summarize, it is not heuristic to label a motor pattern as either instinctive or learned. This kind of labeling closes the door to the investigation of how motor patterns develop. Investigation of how motor patterns develop often reveals an interesting blend of instinctive and learned components. Some motor patterns genuinely are closed. They exist in their final form when the animal hatches or is born. But in many instances, and really to an unknown extent, motor patterns become modified by environmental input to which the animal's nervous system has a programmed sensitivity.

If not Motor Patterns, how about Responses to Stimuli?

A nature-nurture adherent at this point might object, noting that I have focused on motor patterns, or motor output, and that I have not considered stimulus and response. Perhaps animal responses to stimuli might be either instinctive or learned. This is a reasonable objection. However, when we study the development of responses to stimuli, we see the same patterns that exist for the development of motor patterns. Some responses are indeed "hard wired" and unvarying, but many develop through an interesting blend of instinctive and learned components. I will give an example of each.

Where Do I Drink?

When bats are out forging, plucking insects out of the night sky, they also need to drink. They drink by flying low across the surface of a river or lake and dropping the jaw to scoop water. In the dark, how can an animal with very weak eyesight identify a body of water?

This was the question that researchers at the Max-Planck Institute for Ornithology recently sought to answer[38]. The researchers proposed that bats could use echolocation to identify water. When a bat flies over water, most of its echolocating clicks strike the surface and reflect obliquely away, but a small fraction of the sound wave passes straight down and bounces straight back. The echo characteristics of a smooth surface are distinct and different from the echo characteristics of any sort of textured surface.

The researchers thus reasoned that, if bats use the echo properties of water to identify water, they should attempt to drink from any surface that had those echo properties. In nature, no other surface has these properties, but in the laboratory, surfaces like this can be presented to bats. The researchers made artificial water surfaces from metal, wood, and plastic, and made versions of these that had surface texture. In a flight room, they placed one sheet of smooth and one sheet of textured material on the sandy floor, and then released a thirsty bat. The bats attempted to drink from the smooth surfaces and did not attempt to drink from the textured surfaces. In 5-minute trials, bats attempted to drink from the smooth surfaces about 50-100 times, and continued to do so even after they had landed on these surfaces. The researchers then placed the smooth surfaces on a table top in the flight room, to discover if water that appeared to be hovering in midair would be less attractive. Even thought the bats flew underneath the table, (perceptually, flew under water) they continued to attempt to drink from the smooth surface. The researchers ran these tests on 15 diverse bat species and got the same results, suggesting that all echolocating bats identify water using this feature detector.

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[38] Greif, S. & Siemers, B.M. Innate recognition of water bodies in echolocating bats. Nature Communications 1:107 doi: 10.1038/ncomms1110 (2010).

Finally, the researchers captured young bats and their mothers from a cave before the juveniles could fly, and raised them in the laboratory. When the juveniles could fly, they were tested. These animals had never flow over water, but they tried to drink from the smooth surfaces on their first flights in the test room. Bats are born with a feature detector to identify water and they use the feature detector, unmodified, throughout life.

Learning where to Peck

One of the classic studies in ethology concerned the investigation of signaling that coordinates feeding by parents of newly hatched chicks in several gull species. In nature, a gull chick hatches and then spends an hour or so getting dry, its downy coat fluffing up to provide insulation. One or both parents are present to warm the chick if need be, and to shield it from gulls on neighboring territories, who would jump at the chance to devour an unprotected chick. After it is dry and standing, the parent typically regurgitates some food (such as a half-digested fish) into the nest, breaks off a morsel, and holds it in the tip of the beak, which is held at a downward angle toward the chick. The chick pecks at the parent's beak, and eventually strikes the food with a peck, and has its first meal. On this and on subsequent occasions, the chick may peck first at the parent's beak, inducing the parent to regurgitate.

Niko Tinbergen, the Nobel laureate who I introduced in Chapter One, directed the first systematic studies of the pecking response of gull chicks[39]. Tinbergen reasoned that a gull chick could not hatch with a picture of the parent's head in its brain. There must be a simpler set of features about the parent's head that were sufficient to elicit pecking. The features had to be sufficient to provide a target, because the chick reliably pecks near the tip of the parent's beak.

Tinbergen's initial studies, conducted in the Netherlands shortly after the end of World War II, were on Herring gulls. Like many other closely related gull species, adult Herring gulls have a light colored head and a yellow beak that has a conspicuous gonydeal spot, a roughly circular red spot on the lower mandible near the tip. To figure out the key stimulus elements that elicited chick pecking, Tinbergen and his student helpers searched through the gull colony for damp or newly dried chicks that had not yet had a feeding experience with a parent. They brought these chicks to a nearby tent or sheltered spot and presented them with models of an adult gull's head. The models were cut from heavy paper, were painted, and were attached to a short rod that the experimenter could hold and use to move the model head back and forth in front of the chick. During each model presentation, the experimenters counted the number of pecks that the chick aimed at the model. Tinbergen and his coworkers systematically altered the color, size, and shape of the models to discover what aspects of the overall stimulus elicited the pecking by chicks. Besides the two-dimensional paper models, they also made three-dimensional models and in a few

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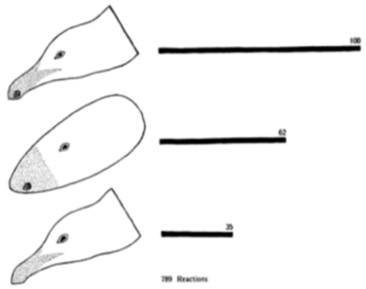
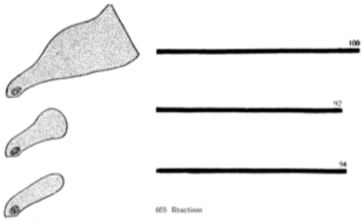
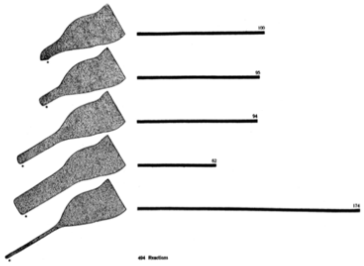
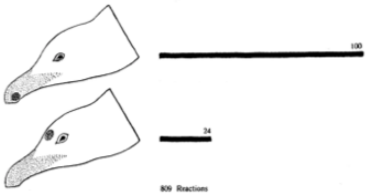
[39] Tinbergen, N. & Perdeck, A.C. 1950. On the Stimulus Situation Releasing the Begging Response in the Newly Hatched Herring Gull Chick (Larus Argentatus Argentatus Pont.). *Behaviour* 3(1), 1-39.

instances presented the actual head of a dead gull. These tests revealed that three-dimensional depth of the stimulus was not important; chicks responded just as strongly to the paper cutouts.

Tinbergen's main results and the nature of the data from which he drew his conclusions are shown in Figure 5.3. The results show that chicks do not hatch with an innate (instinctive) picture of the parent's appearance. Note that the shape of the beak alone is as effective as the shape of an entire head. Chick pecking is elicited most strongly by a moving narrow rectangle that has a dot of contrasting color near the tip. Chicks hatch, not with a picture of the parents in their heads, but with a feature detector. The behavior of the parents and the appearance of the parental beak turn on the feature detector. When Tinbergen homed in on this constellation of stimulus characteristics (to ethologists, the effective constellation was called a Sign Stimulus), he was able to construct an exaggerated version, a very thin strip with contracting color near the tip, that elicited more pecking than a complete model of a parent's head. He had constructed what ethologists referred to as a Supernormal Stimulus. Experimenters can construct Supernormal Stimuli because animals commonly rely on feature detectors to guide their behavior.

	Two –dimensional paper models: The shape of a gull head with the red spot on the beak elicits more pecks than a correctly colored, misshapen head. A normally shaped and colored head that is missing the red spot receives the least number of pecks
	Two dimensional paper models: A beak-like shape with the red spot elicits as much packing as the shape of an entire head
	Two-dimensional paper models: A head shape with an abnormally long thin beak (bottom) elicits more pecking than the normal shape or a head shape with a thicker beak
	Two-dimensional paper models: This is the most famous of Tinbergen's results – a normally shaped and colored head elicits many more pecks than a normally shaped head that has the red dot moved to the forehead

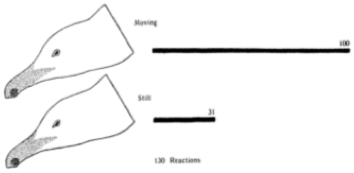
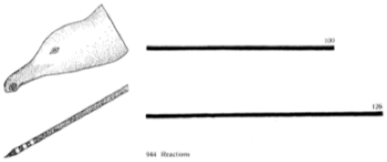
	Two dimensional paper models: A normally shaped and colored head that is moving elicits many more pecks than the same model that is not moving
	Two dimensional paper models: A supernormal stimulus. A very thin rectangle with contrasting colors near the tip elicits more pecks than a normally shaped and colored head.
	A herring gull chick pecking at the supernormal stimulus

Figure 5.3. Some of the models that Tinbergen and his coworkers used to study the stimulus characteristics that elicited pecking by newly hatched herring gull chicks. The length of the bar beside each model represents the strength of the chick's pecking response to the model. Figures reproduced from: Tinbergen & Perdeck (1950). On the Stimulus Situation Releasing the Begging Response in the Newly Hatched Herring Gull Chick (Larus Argentatus Argentatus Pont.). Behaviour 3(1), 1-39.

Tinbergen, with the lucidity that characterized his perception and thinking, correctly depicted the signaling system between the parent and chick. Chicks hatch with an instinctive feature detector that guides their pecking. The feature detector is turned on most strongly by a moving narrow rectangle that has a contrasting spot of color near the tip. Chick pecking induces the parent to regurgitate food. Recently, researchers in the Netherlands replicated Tinbergen's studies, using more stringently controlled methods, and confirmed his results[40].

Tinbergen's conclusions were incorrect in only two respects, one somewhat trivial and one more important. The trivial error was that Tinbergen concluded that the relative position of the red spot on the parent's beak was important. Note in Figure 5.3 that the model with the red spot on the parent's forehead elicits less pecking than the model with the red spot in the normal position. Tinbergen's interpretation of this result was that the chick hatched with a kind of rudimentary image in its brain, that included the correct position of the red spot. About two decades after Tinbergen conducted his research, an American, Jack Hailman, proved that this interpretation was incorrect[41]. Working from a suggestion made by others, Hailman tested the hypothesis that the important part of the red spot stimulus was its angular velocity, how quickly it swept through an arc in front of the chick, not its overall position in the gestalt of the parent's head. To test this hypothesis, Hailman attached a longer stick to the model with a red spot on the forehead, so that the forehead

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[40] ten Cate, C., Bruins, W.S., den Ouden, J., Egberts, T., Neevel, H., Spierings, M., van der Burg, K. & Brokerhof, A.W. 2009. Tinbergen revisited: a replication and extension of experiments on the beak colour preferences of herring gull chicks. *Animal Behaviour* 77, 795-802.

[41] Hailman, J.P. 1967. The Ontogeny of an Instinct: The Pecking Response in Chicks of the Laughing Gull (Larus atricilla L.) and Related Species. Behaviour Supplement 15, 1-159.

red spot had the same angular velocity as the beak red spot on the normal model. Chicks pecked at this adjusted model at the same rate as at the normal model (Figure 5.4). The significance of this work was to reinforce the conclusion that animals do not come into the world with pictures, even rudimentary pictures, encoded in their brains. Rather, they come equipped with feature detectors, that allow them to respond appropriately to the relevant objects in the bright buzzing world.

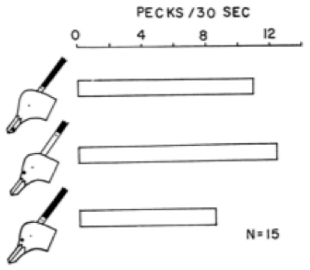
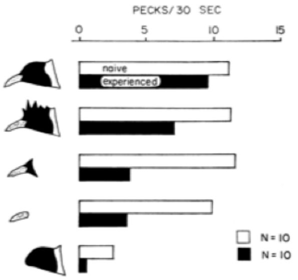
	A two dimensional model with the red spot moved to the forehead and presented as Tinbergen did (bottom) elicits fewer pecks than a model with the spot in the correct location (top). If the model with the red spot on the forehead is attached to a longer rod (middle), so that the angular velocity of the red spot equals that of the normal model, the rate of pecking is not diminished.
	A comparison of the responses of newly hatched chicks (white bars) to the responses of chicks that have been in the nest for several days (black bars). Newly hatched chicks respond to the abstracted stimuli, but experienced chicks have learned to recognize the parent.

Figure 5.4. Results from Jack Hailman's experimental reevaluation of Tinbergen's results. Figures reproduced from Hailman, J.P. 1967. The Ontogeny of an Instinct: The Pecking

Response in Chicks of the Laughing Gull (Larus atricilla L.) and Related Species. Behaviour Supplement 15, 1-159.

The second adjustment to Tinbergen's conclusions that Hailman offered was related, but more significant. Hailman studied the pecking responses of newly hatched chicks and the pecking responses of chicks that had been in the nest for a few days. His results, also shown in Figure 5.4, were stunning. After a chick has fed from a parent for a day or so, it has lost the feature detector-driven response. It no longer will peck at an isolated beak, and it also discriminates between its own and other species. The chick has learned to recognize the parent. So the sign stimulus that Tinbergen worked hard to identify is important. It directs the chick's first pecking responses to the parent, but it is important only for the first day or two after hatching. When the parent delivers food and the chick can see who is feeding it, the chick begins to memorize the exact appearance of the parent. Feature detector-driven response to the parent is replaced by memorized facial recognition of the parent. Responses to stimuli, like motor patterns such as bird song, often develop out of a mixture of instinctive and learned components.

A human baby may smile before it is born, but not because it is happily anticipating the painful squeezing that it about to experience. The baby smiles because the nervous system is rehearsing a motor program that will be used right after birth. After it is born, the baby smiles in response to a face-like object. It will smile at a cardboard face-shaped disc, or at a disc with eyes, nose and mouth in scrambled orientations. Later, like gull chicks, the human infant replaces this feature detector-driven response with a response that is based on memorization of the facial characteristics of its parents.

Chapter Six

Learning

In the Stanley Basin of central Idaho, beautiful Redfish Lake is surrounded by the White Cloud, the Boulder, and the Sawtooth Ranges. The name of the lake derives from the once great numbers of Sockeye salmon that came there to spawn. The males have red backs when they are in breeding condition, and reportedly the surface of the lake had a reddish cast during spawning season. These fish fed and grew in the Pacific Ocean and then, when they were big enough, made their way to the mouth of the Columbia River. They passed through the Gorge, where the mighty Columbia cuts through the Cascade Mountains, and continued west for another 200 kilometers until they reached the great bend in the Columbia, just west of Walla Walla, Washington. There, they turned right and followed the Snake River toward the mountains, and continued to swim up the Snake as it turned south to cut through the towering basalt cliffs that flank Hell's Canyon. In the canyon, a powerful river, the Salmon, joins the Snake from the West. Here, the fish turned left to enter the Salmon and to pass upward through The Eye of the Needle, a steep violent rapid where the Salmon makes its final drop to the Snake. The fish then ascended the Salmon as it passed through a deep gorge in the Idaho Batholith and then turned south, still swimming up the Salmon as it flowed along the West slope of the Bitterroot Range, and up into the Stanley Basin. In the basin, they made a final turn out of the Salmon into a small creek that flowed out of Redfish Lake. They ascended into the lake, having swum about 1,600 kilometers and gained about 2,000 meters in elevation from the mouth of the Columbia. The red males set up their territories in the colorful gravel along the lake shore, and the females made their mate choice decisions, shedding their eggs to be fertilized by the chosen males. All the adults then died, leaving billions of developing eggs in the gravel.

Salmon are anadromous, meaning that they hatch in fresh water, migrate to the Ocean or to an inland sea, and return to fresh water to spawn. All make trips similar to the fish of Redfish Lake, although all other trips from the Ocean are shorter. All salmon show strong home stream fidelity, meaning that adults return to spawn where they hatched. For this reason, salmon runs tend to be closed populations, and tend to show local adaptations[42].

Consider how remarkable the homing performance of salmon is. A tiny smolt, about 8-10 cm long, drifts into a river drainage and descends to the ocean. Several years later this individual, that may have been far at sea, returns to the river mouth where it emerged, and then follows in reverse the turns that it made long ago, until it reaches the stream where it hatched. How do salmon accomplish this extraordinary feat? Arthur Hasler of the University of Wisconsin discovered most of the answer the answer in the mid-twentieth century. Hasler hypothesized that salmon find their way home by smell. Because each stream or lake has its own bedrock, its own surrounding soil, and its own surrounding plant community, each has its own specific cocktail of dissolved chemical compounds. Hasler realized that this could provide the basis for homing, if salmon had a way to memorize the odor of their hatch site[43].

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[42] Taylor, E.B. 1991. A review of local adaptation in Salmonidac, (sic) with particular reference to Pacific and Atlantic salmon *Aquaculture, 98,185-207.*

[43] Hasler, A.D. & Wisby, W.J. 1951. Discrimination of Stream Odors by Fishes and Its Relation to Parent Stream Behavior. *The American Naturalist* 85, 223-238.

Hasler conducted a test of his odor homing hypothesis using Coho salmon that were reared in a hatchery on the shores of Lake Michigan[44]. His team marked many fish and then, in the hatchery, divided the fish into two groups. Into each group's tank, the researchers dripped small amounts of either Morpholine, or Phenethyl alcohol (PEA). These synthetic organic compounds do not occur in natural streams, but the fish are able to detect them at low concentrations. The fish were exposed to these odors for about six weeks, while they were transforming into the migratory juvenile form called smolts. The researchers then transported the smolts to Lake Michigan and released them. Eighteen months later, during the fall spawning migrations, the researchers infused Morpholine into one river and PEA into another river about 10 kilometers down the Lake Michigan shoreline. The fish had initially been released midway between these two rivers. The researchers then monitored salmon returns in the experimental rivers, a well as in 17 other rivers to the North and to the South. The results were extremely clear. About 90 to 98 percent of marked fish were recovered in the river containing the odor to which they had been exposed almost two years previously, when transforming to a smolt. Hasler concluded that salmon are able to home to their natal stream because they imprint to the odor of that stream when they are smolts. Since Hasler's discovery, others have hypothesized, but not proved, that smolts must memorize a series of odor signatures that indicate the other turns that precede the final turn to the home stream.

Imprinting

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[44] Scholz, A.T., Horrall, R.M., Cooper,J.C. & Hasler, A.D.1976. Imprinting to Chemical Cues: The Basis for Home Stream Selection in Salmon. *Science* 192, 1247-1249.

The term, *imprinting*, that Hasler used, was an invention of Konrad Lorenz, one of the Nobel laureates for ethology. As a central part of his research, Lorenz raised and lived with many animals in his home. The geese that Lorenz raised revealed to him the phenomenon of early, rapid, irreversible learning that allows young waterfowl to follow the mother and later to express sexual interest in the correct species. Because Lorenz was the "parent" of several clutches of geese (that is, he was the only moving object present at hatch) he found himself followed by young goslings and later courted by these individuals when they became sexually mature. Lorenz used the term imprinting to denote this early learning because the effect occurs rapidly and seems to be irreversibly stamped on the animal's brain. Later research revealed that there are two distinct processes involved. The first, called filial imprinting, occurs in a short sensitive period shortly after hatch. The young duck or goose memorizes the appearance of the first moving object that it sees, and then forms an attachment to that object. When the object moves away, the juvenile follows. If the juvenile is visually separated from the object, it begins to emit distress calls. In nature, that first moving object is the mother. If inquisitive humans intervene, that object may be Konrad Lorenz, or a toy train, and the duckling will follow those. In most species, sexual imprinting occurs during a later and less sharply defined sensitive period. Nevertheless, sexual imprinting can be potent. For example, sexual imprinting resulted in the failure of the Grays Lake, Idaho Whooping Crane recovery effort, started in 1975 and stopped in 1989. Wildlife biologists wanted to augment the number of endangered Whooping Cranes. Like other cranes and related birds, this species lays a clutch of two eggs, but only one juvenile survives. The biologists charged with the recovery of Whooping Cranes reasoned that they could take this doomed egg from Whooping Crane nests, and have it raised by foster parents. They placed the eggs in the nests of the closely related Sandhill Crane in the Grey's Lake Wildlife Refuge in southeastern Idaho. The Sandhill Crane parents accepted these eggs, raised the young, and showed them the migratory path to the wintering area in New Mexico. As adults, these cross-fostered Whooping Cranes showed no sexual interest in other Whooping Cranes - only in Sandhill Cranes. They had sexually imprinted on the model provided by their foster parents.

Social Bonds

Narrow sensitive period learning also occurs quite often as a way to create exclusive social bonds. Exclusive social bonds are the basis for monogamy. Recall the Prairie Voles that I described in Chapter Four. A male and a female, by copulating, excite reward circuits that guarantee that a bond is formed to the partner. Exclusive social bonds are also the basis for the adaptive provision of maternal care. In the mammals that form large groups, such as most hoofed animals, seals, and bats, a sensitive period that occurs immediately after birth allows the mother to memorize the odor of her young. Learning of the odor signature of young occurs in about the first hour after birth, while the mother is avidly licking the young. If the mother's ability to smell is experimentally blocked during the short sensitive period, the mother does not memorize the odor and will not accept the young. This specialized, rigid, and quite specific form of learning exists to give the mother an infallible ability to identify her own young. This ability is adaptive because milk is very expensive to produce. To maximize her lifetime fitness, a mother should deliver this precious resource only to her own offspring. In the hoofed mammals, mothers also appear to learn, over a few days after birth, to recognize their young visually. Visual recognition serves only as a provisional OK. The mother will allow a juvenile that she recognizes visually to approach, but before she allows the young to suckle, she sniffs under its tail, to be sure that the odor there matches the odor that she memorized in the sensitive period right after birth.

A tougher infant recognition problem exists for some seal mothers, that give birth on a beach and leave the pup behind for days or weeks while they go to sea to feed. Many seal colonies are dense throngs of hundreds to thousands of mothers and young, so when a mother returns to the beach she usually meets with a mosh pit of many hungry pups. To find her own pup she vocalizes, giving what is called the Pup Attraction Call. In contrast to bird song, seal voices do sound like vuvuzelas. A sonogram of the vocalization shows a messy smear of frequencies between about 500 and 2,000 Hz. Nevertheless, there is sufficient individual variation in these vocalizations to allow pups to recognize their own mother's call. Pups call back with a similarly noisy bleat when they hear the mother's call, and mother are able to recognize their own pup's vuvuzela type sound[45]. The vocal signaling allows the mother and young to make initial contact. The mother then sniffs the pup to perform the infallible odor check before she allows it to suckle. Mothers and young memorize these sounds in the day or two immediately after birth, when they call to each other frequently.

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[45] Trillmich, F. 1981. Mutual Mother-Pup Recognition in Galápagos Fur Seals and Sea Lions: Cues Used and Functional Significance. *Behaviour* 78, 21-42.

Charrier, I., Mathevon, N. & Jouventin, P. 2002. How does a fur seal mother recognize the voice of her pup? An experimental study of *Arctocephalus tropicalis*. *Journal of Experimental Biology* 205, 603-612.

The unifying theme in the examples that I have given so far is that animals are able to extract useful information from the environment and to use this information to guide or adjust their behavior in the future. This characteristic of animal brains is called learning. When a salmon smolt memorizes the odor of its home stream, when a duckling identifies and bonds to its mother, when social bonds are formed between mates, or between mother and young, the learning is programmed to operate at the appropriate time and context, and then it is turned off. Other forms of learning are not governed by sensitive periods and they appear to operate throughout life. However, all learning is programmed insofar as what animals learn, the context in which learning occurs, and how rapidly learning and forgetting happen, are all preset. There is no Tabula Rasa. Brains can only learn because they are built with specific learning instructions.

What to Eat and What Not to Eat

The Norway Rat, a source of human misery and disease for centuries, originated in China. The species in nature lives in complex burrow systems that contain related females and young that are guarded by a single male. The species is a generalist feeder, meaning that it consumes many kinds of foods, including fruits, seeds, plant leaves and stems, and small animals. These two characteristics allowed rats to expand into a new niche, commensal living with humans. The spaces beneath human dwellings or within the walls simulate burrows, and a generalist feeder had no trouble adapting to the food sources offered by human households and agriculture. Rats were commensal with humans in China, and reached Europe in ships when trade between the East and the West began.

Generalist feeders like rats have feeding traits that allow them to continually add new items to the diet. When a foraging individual finds something new that might be food, it eats a tiny amount of that and then resumes feeding on known substances. However, the animal forms a memory of the novel smell and taste. If, in the next few hours, the rat becomes nauseous, the rat develops a strong aversion to the smell and taste that it memorized. This specialized ability is called one-trial food avoidance learning. The phenomenon was first described in laboratory strains of the Norway Rat (the characteristics that allowed rats to become commensal with humans allowed humans to domesticate them as laboratory animals). Researchers gave laboratory rats a novel, palatable food and then exposed them to moderate doses of X-radiation. The nausea that was produced by radiation sickness induced avoidance of the novel food.

Rats are also able to acquire preferences for novel foods from each other. Recall that these animals live in extended family groups in burrows. When a forager returns to its burrow, it is commonly greeted by other rats in a short bout of nose-to-nose sniffing. In the laboratory, this sniffing allows individuals to detect the scents of new food on the breath of the returning forager, and causes them to develop a new preference for food bearing that scent[46]. This social acquisition of a food preference for a novel food occurs rapidly and its effect is robust. The context in which this social learning operates in nature is unknown,

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[46] Galef, B.G. Jr. 1993. Functions of social learning about food: a causal analysis of effects of diet novelty on preference transmission. *Animal Behaviour* 46, 257-265.

but it is reasonable to surmise that social acquisition of food preferences, like one-trial food avoidance learning, is part of the learning package that supports a generalist feeding habit. Both forms of learning are ways in which individuals can continue to broaden the diet.

Neophilic Ravens

Another spectacular example of timed, programmed learning that exists to promote optimal diet breadth occurs in common ravens. Raven are one of the most pronounced habitat and diet generalists among perching birds. The species occurs from arctic tundra, to mountains, to seashores, to deserts and even to human cities, and, across these habitats, individuals consume a huge variety of foods. However, adult ravens, unlike adult rats, are neophobic. They avoid and appear to be afraid of food items that they have not previously encountered. Bernd Heinrich, who has studied ravens more than any other biologist, designed an experiment to investigate this paradox[47]. How can ravens be generalists if adults are afraid of new foods? The answer, Heinrich discovered, was in the demeanor of juvenile ravens.

Unlike adult ravens, juvenile ravens have a profound neophilia, which Heinrich demonstrated in a very compelling way. Working with four hand-reared young ravens, Heinrich began each morning session by feeding the young birds as much meat as they wanted. Then he opened the door to the outdoor aviary and led the birds into an arm-like extension of the aviary, that had a natural floor of grass and dead leaves. Initially, Heinrich

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[47] Heinrich, B. 1995. Neophilia and exploration in juvenile common ravens, *Corvus corax. Animal Behaviour* 50, 695-704.

simply recorded which objects the young birds picked up and manipulated in the beak, and which they ate. Then, in subsequent trials he began to add new items, some edible and some inedible. The birds initially picked up essentially every class of object that was in the arena. Then, when new items were added, the birds instantly switched from what they had previously investigated to the new items. If the new items were edible, the birds quickly developed a preference for them, but continued to investigate new items. This ability to find new items, even tiny ones, was extraordinary. At later ages, the same birds showed aversion to novel items. Thus, ravens are programmed to show an intense attraction to novel objects during what is likely a sensitive period in development, at a time when they would be following their parents after leaving the nest. During this time, they learn to discriminate between the edible and the inedible, and they retain the developed preferences for life. The abilities of young ravens to remember every class of object that they have already handled and consequently to instantly recognize novelty presents a huge challenge to neuroscientists. How can a bird with a brain the size of a grape store and instantly recall such a massive amount of information?

Faces

Another example of specific, rapid, directed learning occurs in humans. This is the almost instantaneous formation of a memory for the face of another human. The ability of humans to perform this task rivals speech processing and production for the sheer complexity of the information storage and retrieval involved. Humans can remember thousands of individual faces and can recognize a face seen 20 years previously and altered by age. Like many forms of learning, facial learning occurs automatically, without the need for any specific reward or punishment. Nor is any conscious effort required. Facial learning is a program that starts running it the background whenever we perceive a face.

Facial learning is also a distinct mechanism, that operates independently from the mechanisms that produce object recognition. The conclusion that facial recognition in humans might be a distinct "cognitive module," with its own dedicated area of the brain, was first suggested by the disorder, prosopagnosia, in which humans lose the ability to learn or recognize faces. Prosopagnosia was associated with damage to an area of the temporal lobe of the cerebral cortex called the fusiform gyrus. Subsequent work using functional magnetic resonance imaging (fMRI) identified a region, now called the fusiform face area, that is active when humans view faces. Humans with prosopagnosia have no difficulty recognizing objects, and humans with object blindness have no difficulty recognizing faces[48]

Locations

Another kind of learning that, like facial learning, is programmed to run automatically, without any associated punishment or reward, supports the ability of animals to remember locations and to select efficient travel routes. Like facial learning, spatial learning has its own dedicated brain area, called the hippocampus. The hippocampus performs functions other than spatial memory, but spatial memory is centered there. In the hippocampus are

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[48] Moscovitch, M., Winocur, G., & Behrmann, M. 1997. What is special about face recognition? Nineteen experiments on a person with visual object agnosia and dyslexia but normal face recognition. *Journal of Cognitive Neuroscience* 9, 555-604.

neurons called place cells. Each place cell is assigned to a physical location in the environment that the animal has visited. When the animal returns to that location, the associated place cell becomes active. The automatic assigning of place cells in the hippocampus to physical locations in the environment allows animals to develop what has been called a cognitive map: a mental representation of points in space and their physical proximity to each other. Several comparative studies have shown that species that perform complex spatial memory tasks have a hippocampus that is relatively larger than the hippocampus of closely related species that do not perform such tasks, and that the size difference is associated with longer retention of spatial memories. Even with a species, the hippocampus can increase in size in response to increased demands for spatial memory. London taxi drivers that have worked for several years have a larger posterior hippocampus than control subjects who do not need a detailed spatial map for their work[49]. The concept of cognitive maps is somewhat controversial, because researchers have difficulty defining this term with precision. However, it is obvious that many animals store spatial information in some way and use the information to accomplish important goals.

Several species of birds and mammals that eat seasonally abundant seeds have evolved a way to harvest and store the seeds for use during months when the seeds are not available. Within these so-called hoarding species, there are two distinct hoarding strategies. Larder

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[49] Maguire, E.A., Gadian, D.G., Johnsrude, I.S., Good, C.D., Ashburner, J., Frackowiak, R.S.J. & Frith, C.D. 2000. Navigation-related structural change in the hippocampi of taxi drivers. *Proceedings of the National Academy of Sciences of the United States of America* 97, 4398-4403.

hoarders, such as golden hamsters or acorn woodpeckers, place all the seeds that they harvest in a single defended location. This strategy is simple and easy to carry out, but it is only as good as the ability of an individual animal to defend the larder from thieves. When a larder can't be defended, or when the cost of defending is excessive, species use another strategy, called scatter hoarding. Scatter hoarders, such as grey squirrels, many kangaroo rats, and several species of jays, harvest many seeds but disperse them into dozens to thousands of small isolated caches. A scatter hoarder avoids the risk of losing the entire larder to a thief, but of course must be able to remember all or most of the cache locations. Although it may seem improbable that an animal can remember, in some way, thousands of individual locations in space, scatter hoarders do just that.

Clark's Nutcracker, first described scientifically by the Lewis and Clark Corps of Discovery, is a stout jay of western North America. The species is specialized to exploit the seeds of Pinyon Pines. In fall, individual birds harvest the large seeds, cram them into a specialized pouch in the throat, and transport them to high elevation spots. They may fly more than 20 kilometers to reach these sites where they the cache the seeds. Individuals use the powerful beak to thrust seeds into the ground, creating caches of 1 to 14 seeds. In a year when the pines are productive, a single bird caches 20,000 - 30,000 seeds in 7,000 dispersed locations. In winter and spring, the birds return to their caches to feed themselves and their nestlings. Thus, birds often dig through snow to recover the seeds from a cache. Because snow obscures all local landmarks, it is obvious that the birds have some kind of mental representation of the spatial array of their own caches. Because each cache is created in about 30 seconds, these spatial memories are formed rapidly. Like ravens, Clark's Nutcrackers pose a huge challenge to neuroscientists. How can a bird with a brain the size of a kidney bean store such a massive amount of information? The fusiform face area in humans represents a mass of neural tissue equivalent to several dozen bird brains.

Even greater speed in the formation of a spatial memory is attained by pronghorn mothers when they and their fawns are practicing the hiding strategy. Recall from Chapter Three that at the end of a reunion, a mother gives the fawn a signal and the fawn walks away to find a place to recline. While the fawn is searching for its spot, the mother is usually walking away at an acute angle, apparently intent on the grass in front of her. However, when the fawn begins to recline, bending its long front legs to rest on its wrists, the mother rapidly swings her head to stare directly at the fawn. In another second, the fawn lowers its rear end and it sinks out of sight in the grass. The mother continues to stare at the spot where the fawn reclined for about two more seconds. Then she turns away and usually runs away. She will be away from the fawn for the next three hours, but she knows precisely where the fawn is. This is evident by her pattern of movements around the fawn's location, by her reactions to coyotes that move in the vicinity, and by her return to the original reclining spot when a fawn, because it is sick, has gotten up and moved. Because I want to capture fawns to handle them for about two minutes, I have learned, over many years, to perform a version of what pronghorn mothers do. However, for me to memorize a spot in apparently featureless grassland requires a steady ten minute of so of careful study through a telescope. I need ten minutes to accomplish an imperfect version of what pronghorn mothers do in three seconds. The other impressive aspect of spatial memory by pronghorn mothers is their ability to forget. When a mother returns to her fawn, she leads it away and eventually signals it to choose a new spot to recline. Then the mother forms a new, perfect spatial memory and obviously erases the previous one. There can't be any ambiguity about where the fawn is. The instantaneous formation of a highly accurate spatial memory and the replacement of this memory at three hour intervals is another example of the varied forms of highly specialized, directed, context-specific learning that evolve to help animals achieve their reproductive goals.

Habituation

Some forms of learning have a more general character. They operate throughout an animal's life because they are involved in adjustment to a persistently changing environment. Although nature may seem constant (year after year, you can visit a natural area and detect no obvious changes), it is in constant flux. Food, predators, competing species, and sources of shelter all come and go. Because of the flux, one of the key challenges that animals face is novelty. A new stimulus may represent danger, it may represent a new feeding opportunity, or it may indicate nothing of importance to the animal's fitness.

To maximize fitness, an individual should attend to a novel stimulus to gain more information, but if the stimulus falls into the "nothing significant" category, the animal should stop responding, to devote time and energy to the activities that enhance fitness. The type of learning that accomplishes this task is called habituation. Habituation is defined as the waning of responsiveness to a neutral stimulus. Neutral means that the stimulus is indicative of an event that has no positive or negative effect on fitness. Habituation is ubiquitous in animals, because of the overwhelming importance of staying "on task," and not wasting effort.

The existence of habituation suggests a couple of unknowns about animal nervous systems. First, habituation, like food learning in juvenile ravens, depends on the ability of the animal to perceive a novel stimulus correctly: that is, as something not encountered previously. How brains are set up to keep track of what has been encountered previously and what has not, or, put in another way, how novelty is identified, remains unknown. Second, habituation depends on sensitive fitness meters. We know about the coarse scale fitness meters, such as pain and the reward pathway, but in nature, animals come across many new things that are neither painful or rewarding, and they need to have a way of deciding whether these new things really are neutral. Whether there are other fitness meters, more subtle than pain and reward, is an open question.

The existence of habituation is sometimes useful to experimenters. For example, to discover what instinctive discriminations between speech sounds human infants make, researchers commonly measure the rate of suckling on a pacifier as an indicator of habituation. Then, when a new speech sound, that the infant can discriminate as different, is presented, the suckling rate rebounds. Habituation thus allows researchers to ask newborn infants questions about the differences in speech sounds that they can hear. For example, using the sucking rate design, researchers showed that infants can discriminate between spoken Japanese and spoken Dutch, but not between these languages when they were played in reverse[50]. Interestingly, individuals of a New World monkey species were able to make the same discrimination.

The existence of habituation also presents a technical problem for researchers who perform experiments in the field or in the laboratory. For example, suppose that you wanted to test the hypothesis that females in a frog species were more attracted to males that emitted call type A than to males that gave call type B. Using recordings of calls you play call A to a series of individual females and measure the rate at which they approach the loudspeaker. Then you play call type B to the same series of females, measure the rate of response, and get a significantly lower value. You are inclined to accept the hypothesis that females prefer call type A, but your results are also consistent with no difference in preference: the result could simple reflect habituation to the recorded calls. The existence of habituation forces researchers to think carefully about the order of treatments when they design experiments.

Pavlov

At the start of the twentieth century, a Russian physiologist named Ivan Pavlov investigated what he referred to as physiological reflexes. In one preparation in Pavlov's laboratory, a dog was restrained by a harness to stand on a table. Days or weeks earlier, Pavlov had cut through the dog's cheeks to insert and to sew into place a cannula (glass

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[50] Ramus, F., Hauser, M.D., Miller, C., Morris, D., & Mehler, J. 2000. Language Discrimination by Human Newborns and by Cotton-Top Tamarin Monkeys. *Science* 288, 349-351.

tube) that provided access to each side of the dog's mouth. The physiological reflex that Pavlov studied was the dog's release of saliva into the mouth in response to food. Pavlov could blow a puff of meat powder through one cannula and then measure the volume of saliva that dripped from the other cannula into a graduated cylinder. Pavlov referred to the meat powder as the Unconditioned Stimulus and to the production of saliva as the Unconditioned Response. Then Pavlov began to introduce another stimulus, such as a bell ringing, that would appear coincidently with the puff of meat powder. After several trials, in which the stimuli appeared simultaneously or nearly so, it became possible to induce the production of saliva by presentation of the bell alone. The dog would salivate even though no meat powder was in the mouth. Pavlov referred to the ringing bell as the Conditioned Stimulus, and to salivation in response to the bell alone as the Conditioned Response. The entire procedure is now known as Pavlovian Conditioning, or Classical Conditioning.

An important characteristic of Pavlovian Conditioning is that the dog (and any other animal that can be trained in this way: fruit flies, for example) is not stupid. If the bell (Conditioned Stimulus) is presented alone, without the meat powder in the mouth (Unconditioned Stimulus) for several trials in a row, the production of Saliva in response to the bell (Conditioned Response) begins to wane and eventually goes away. Pavlov referred to this unlearning of the Conditioned Response as Extinction. Any stimulus that the dog can perceive will work as a Conditioned Stimulus, and punishing Unconditioned Stimuli, such as sources of pain, are as effective as rewarding Unconditioned Stimuli, such as food. The existence of Pavlovian Conditioning means that animals are able to temporarily assign previously insignificant events (such as a bell ringing) that are reliably associated with pain or reward as indicative of pain or reward and to respond appropriately. When the association between the stimulus and the fitness-related event goes away, the animal begins to forget the association.

The mechanisms that produce Pavlovian Conditioning also produce what is called Instrumental Learning. In Pavlovian Conditioning, the animal begins to associate the Conditioned Stimulus (bell) with the Unconditioned stimulus (food). In Instrumental Learning, the animal begins to associate some behavioral act that it performs with the Unconditioned Stimulus. For example, a psychologist builds a cage for a rat that contains a metal bar on a spring-loaded hinge and a small trough below. When the rat presses the bar, a food pellet drops into the trough. A rat will quickly develop a bar pressing response. A psychologist builds a cage in which one half of the floor is made of metal bars that can carry an electric current to shock the rat's feet. If a Conditioned Stimulus such as a light or a bell is paired with the shock, the rat will quickly learn to run to the other side of the cage when the Conditioned Stimulus is presented. Like responses built up by Pavlovian Conditioning, responses built up by Instrumental Learning also show Extinction when the pairing between the behavioral act and the punishment or reward is removed. The existence of Pavlovian Conditioning and Instrumental Learning means that animals have evolved mechanisms to associate events in nature or acts that they do with important fitness outcomes. The association allows them to modify their behavior appropriately to promote events that cause fitness gains and to avoid events that cause fitness losses. These two general forms of learning, active throughout an animal's life, exist because the nature is constantly in flux. In one year, heavy rains mean that a preferred food plant will be found in particular locations, but in other years, the plant will not be there. A new species of predator moves into the area where you live, and then later moves away. Flowers that a nectar-foraging animal such as a honeybee appear and bloom and then disappear.

Even though Pavlovian Conditioning and Instrumental Learning seem general, they are not, entirely. What an animal can learn and how fast it can learn are influenced by its overall behavioral repertoire. For example, learning in rats, as I suggested, often is studied by measuring the bar pressing response. Learning in pigeons (the bird version of the laboratory rat to psychologists) is studied by measuring the rate at which the individual pecks at a target. These responses are easy to elicit in training that involves a food reward because rats commonly manipulate food with the forefeet, and pigeons gather food items from the ground by pecking at them. It is very difficult if not impossible to train a rat to peck for a reward, or to train a pigeon to push a bar with a foot. Now, consider a more subtle but more revealing example. Hummingbirds feed by hovering in front of a flower, inserting the beak, and using the tongue to lap the few microliters of nectar that the flower offers. In the laboratory, researchers trained individual hummingbirds of a few different species to a simple task[51]. The bird had to fly to a perch. When it alighted, it was presented with two artificial flowers on the other side of the room. The bird was allowed to sip from one flower, then had to return to the perch before it could drink again from either flower. The researchers trained the birds in “switch” learning, meaning that, to be rewarded at the second visit to a flower, the bird had to visit the other flower, not the one that it had just visited. The researchers also trained the birds in “stay” learning, meaning that to be

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[51] Cole, S., Hainsworth, F.R., Kamil, A.C. Mercier, T. & Wolf, L.L. 1982. Spatial Learning as an Adaptation in Hummingbirds. *Science* 217, 655-657.

rewarded at the second visit to a flower, the bird had to return to the flower that it had just visited. All birds were trained at both tasks. One group learned switch first and then stay. The other group learned stay first and then switch. Although these tasks seem equivalent to us, they are not equivalent to a hummingbird. In the study, the researchers found that it was relatively easy to train the birds to switch learning, and very difficult to train them to stay learning. This difference in learning rates occurred because of the natural foraging behavior of hummingbirds. In nature, a bird depletes the nectar from one flower and then moves on to another flower. An individual maximizes its rate of energy harvest specifically by *not* returning to a flower that it has just visited. Thus, in switch learning, the researchers were asking a bird to learn to do what it does in nature, and in stay learning were asking it to override it natural foraging preference.

Instrumental learning is what happened when Clever Hans became an apparent mathematician. His owner unconsciously trained him when to start and when to stop pawing with a forefoot. Unconscious instrumental learning by owners is also the basis for nearly all the problem behavior of pets. Instrumental learning is the basis for what all animal trainers do. At a dog show, notice that the handler holds a food reward and shows it to the pet. All of the dog's postures, reactions to cues, and gaits are carefully trained responses. The handler used instrumental learning with food rewards to create them.

Chapter Seven

Moving Through Space

Path Integration

On a dark, moonless night in the Syrian desert, a female golden hamster emerges from her underground burrow. She pauses, with only her head above the burrow mouth, for several minutes. This pause allows her a reasonable chance to detect predators that may be lurking nearby. Then, she trots into the dark. She is foraging for the seeds of desert plants. As she finds seeds, she pushes them into her large cheek pouches, which allow her to pick up a huge load of seeds before the trip back to the burrow, where she will add to the larder hoard. Her foraging takes her on an erratic path. She flits here and there, following promising scents. Her foraging trip may last for an hour or more and carry her several hundred meters away from her burrow. When her cheek patches are filled, or when her aching mammary glands tell her that it is time to return to her hungry pups, she runs along an almost straight path back to the burrow entrance.

How does she accomplish such accurate homing? There are no visual landmarks because the sky is cloudy and dark. There may be some chemical signposts, left by the female when she smeared her flank glands on rocks, but these would not indicate the straight line vector back to home. There are no detectable sounds coming from the burrow. Despite the absence of any useful external cues, the female, at the outbound end of her erratic foraging path, somehow "knows" the direction in which the burrow lies.

At this point, you may not be too surprised by the hamster's homing ability. You may conclude that it seems natural that the hamster would know where home is, because you intuitively sense the same ability in yourself. Blindfolded, and wearing noise-canceling headphones, you could walk some distance, make a number of turns, and then accurately point to your starting position.

This mysterious ability in you, the hamster, nearly all vertebrate animals and in many invertebrate animals, is called path integration. Consider a simple example. You leave home and travel due East for 10 meters. Then you turn 90 degrees to the left and travel due North for 10 meters. Where is home now? It lies precisely to the Southwest of your current location, and by the Pythagorean Theorem, is at a distance of 14.14 meters. To know where home is, all you need to do is to maintain a running sum of all your travel vectors, and be able to perform the equivalent of trigonometry. Carefully controlled experiments in the laboratory proved that hamsters can find home accurately when all other sources of sensory information are blocked.[52]

In the vertebrate animals, there are three sources of information about travel vectors. First, and most importantly, there is the vestibular sense, provided by the saccule, utricle, and the three semicircular canals in the inner ear. These fluid-filled organs contain sensory

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[52] Siegrist, C. Etienne, A.S., Boulens, V., Maurer, R. & Rowe, T. 2003. Homing by path integration in a new environment. *Animal Behaviour* 65, 185-194.

cells, each with a hair-like filament that projects into the fluid space. The slightest movement of the head causes these filaments to sway, and this movement is transduced into action potentials. Information from the vestibular organs provides very detailed information that the brain computes as acceleration in any direction. The second source of information about travel vectors is the touch sensation, created when the animal pushes against the ground, air, or water to propel itself. The third source of information is a reference copy of the motor commands that go to muscles. These three sources of information are integrated to provide detailed and accurate information about the direction and distance of travel segments. In the vertebrate animals, it is also now established that the brain area where this self-referential information is put together and used to compute where an individual is with respect to any previous start point is the hippocampus, the same area that produces cognitive maps.

Path integration is another example of a specific, reward-free learning program that operates in the background, whenever an animal moves. It is the primary sense that supports nearly all the moment to moment movements that animals perform. Animals always “know” where they are with respect to where they have just been. It is difficult to overemphasize the importance of this ability, even for animals that do not have a home location.

Landmarks

The invertebrate animals do not have the fancy vertebrate vestibular system and so must rely on less precise mechanisms of path integration.[53] Their more error-prone path integration gets them at least to the vicinity of home, where another class of cues, landmarks, become useful. Niko Tinbergen published a now classic demonstration of this phenomenon[54]. Tinbergen worked on the bee wolf, a solitary wasp that digs a burrow in sandy soil, and then hunts for a bee, that will become the paralyzed meal upon which she lays her egg in the burrow. Tinbergen's sensitive powers of observation allowed him to notice that the wasp, when leaving to hunt, always flew in rough circles around the burrow for a few moments before flying away in search of a bee. Tinbergen hypothesized that the circling flight was designed to allow the wasp to memorize landmarks close to the burrow entrance. He tested the hypothesis with his characteristic wit: he placed pine cones in a ring around a burrow while a female was inside. The female emerged, performed her orientation flight, and flew away. Tinbergen then moved the ring of pine cones about one foot away from the burrow. When the female returned, she searched only within the displaced ring, one foot away from the plainly visible burrow entrance. She was able to find her burrow only after Tinbergen moved the pine cones back to their original location. There are thousands of solitary bee and wasp species, in which a female constructs a nest, provisions it, lays an egg, and seals the entrance, all on her own. In these species, landmark learning is almost certainly the way that individuals re-find the nest entrance after a trip away.

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[2] Muller, M. & Wehner, R. 1988. Path integration in desert ants. *Proceedings of the National Academy of Sciences of the United States of America* 85, 5287-5290.

[54] Tinbergen, N. 1951. The Study of Instinct. Oxford University Press, Oxford. In this classic book, Tinbergen gives an English summary of these early 1930s studies, which were published in Dutch.

Sun Compass

Three European ethologists received the Nobel Prize in Medicine in 1973. I mentioned Konrad Lorenz in Chapter One, and I have had quite a bit to say about Niko Tinbergen. Now it is time to introduce the third Nobel Laureate, Karl von Frisch, who discovered what he called the dance language of honeybees, and in doing so proved that insects can use the sun azimuth to navigate.[55]

Bees are a derived group of wasps that have abandoned the use of insect prey as meals for their developing brood, feeding their young instead with nectar and pollen collected from flowering plants. Like the wasps, most bee species are solitary; each female on her own excavates a brood chamber, lays eggs, and provisions the larvae with food collected from flowers. A few species of bees are social: several females jointly lay eggs and work in a common brood chamber. A very small number of bee species are what is called eusocial. In eusocial species, the living and reproductive arrangement involves a very large group of females, in which one or a few individuals lay eggs, and most do not, acting instead as workers, that build, repair, clean, care for brood, collect food, and guard. The eusocial epitome is the honeybee, *Apis mellifera*, which lives in colonies of thousands of individuals. In a honeybee colony, there is one reproductive female, the queen, that lays all the eggs. Nearly all the other colony members are sterile female workers. A few males hang around, begging for handouts, and doing no work. The extreme sex ratio skew is possible because

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[55] von Frisch, K. 1973. Decoding the Language of the Bee. Nobel Lecture, December 12, 1973.

the bees, descended from wasps, have haplodiploid sex determination, and the queen mostly lays fertilized eggs.

Honeybee workers secrete sheets of wax from between their abdominal plates. They chew the wax to make it malleable, and then they construct comb, a vertical, two-sided sheet of hexagonal cells. Each cell lies almost horizontally, with its mouth facing just slightly up, and it is backed by another cell facing in the opposite direction. Because the cells are hexagonal in cross section, they can fit together in a continuous sheet, sharing common walls with no wasted construction material. The diameter, depth, and wall thickness of all cells are essentially identical. Wild honeybees build comb in natural cavities, such as hollow trees. They seal the construction cavity with a glue like substance called propolis, that creates a watertight, airtight, antibacterial seal around the dark hive cavity. A hive thus has a single entrance, and this entrance is guarded by workers that check the odor identity of each entering bee. Individuals that bear the colony odor signature are allowed to pass. Any other bee or other insect species is attacked and usually killed. Vigorous colony defense is needed because the colony represents a highly energy-dense food resource. Each comb cell is filled with a developing egg or a larva or pupa (a brood cell), or it is packed with pollen or honey. The mass storage of vast amounts of food allows the entire honeybee colony to survive through winter, with mature workers ready to harvest nectar and pollen from the first flowers of spring. Honeybees are able to collect huge amounts of food because a colony sends many workers out each day to forage for nectar and pollen, and because the individuals are able to help each other to find food. The workers help each other by communicating the location of rich food sources. They do this by the dance language discovered by von Frisch.

Von Frisch made his astounding discovery using keen powers of observation, inspired hypothesis formulation, and some very inventive design of hypothesis tests. The innovation that started the process of discovery was the observation hive. Von Frisch discovered that he could build a tall narrow box that bees would accept as a nest cavity. Further, he discovered that he could use a pane of glass as one of the wide sides, as long as he kept the glass covered most of the time. Then, to observe the bees going about their natural behavior inside the hive, von Frisch could sit on a stool in front of the glassed side, and remove the cover. The bees would continue to act normally. When you first see such an observation hive, you perceive what looks like chaotic activity. There are bees hurrying in all directions; each bee is intent on the particular task that she is carrying out at the moment. This could be feeding larvae in brood cells, building comb, carrying out trash, and so on. What you, the observer, see is a mad scramble. However, if you have von Frisch's keen observational power, you may notice small clusters of bees. Each cluster comprises several individuals that form a circle around a single bee. The single bee is moving quickly in mirror-image half circles. She walks in a right-turning semicircle from 12 o'clock to 6 o'clock, then moves in a straight line back to 12 o'clock (up through the center of the clock face), rapidly swinging her abdomen from side to side, while elevating her wings slightly and vibrating them. Then she turns left and walks in another semicircle to 6 o'clock, does her waggle run back to 12 o'clock, turns, right, and so on. Von Frisch called this performance a bee dance.

A dancing bee performs for several minutes, and, during the performance, the straight line of the waggle run always points in the same direction with respect to the vertical. The circle of bees that surrounds a dances crowds in close, so that their antennae can touch the dancer. The information that the observing bees are noting is first, the angle between the vector of the waggle run and the vertical, and second, the length of the waggle run. Both pieces of information are important. The dancing occurs on comb inside the hive, and thus normally in the dark. That is why the observing bees press in close. They are getting the information by feel.

Von Frisch also invented the technique of experimental feeders. He showed that he could set out a small glass dish of sugar water and the bees from his hive would come to it. While a bee was busy pumping her crop full of sugar water, von Frisch could apply a dot of paint to the top of the bee's thorax. Away from the hive, bees are not aggressive, and they tolerate being pushed around by a paint brush.

Figure 7.1. Karl von Frisch and his wife marking bees at an experimental feeder

Then, back at the hive, von Frisch observed that the painted bees were dancing, and he realized that the dance must be some form of recruitment to the rich food source that the forager had just found. Evidence that such communication was happening was revealed by the increasing numbers of workers that showed up at the feeder after the dancing started. Von Frisch then set out several feeders, at different directions and distances from the hive. At each feeding site, he painted bees with a unique color. Back at the observation hive, he noticed that bees of all the colors corresponding to the different feeders were dancing and then, quite observantly, noted that all bees of the same color danced with the same angle of the waggle run with respect to the vertical. Von Frisch was able to accurately measure the angle between the vector of the waggle run and the vertical by laying a protractor against the glass. A weighted plumb bob was attached to the center of the protractor. Von Frisch could thus rotate the protractor until its bottom edge lined up with a waggle run, and read the angle. All bees of another color danced with another specific angle between the waggle run and the vertical. This was the key observation. Von Frisch realized that this angle must convey some information about the direction of the food source. Then, von Frisch made the final key observation. Bees painted the same color slowly changed the direction of the waggle run as the day wore on. The direction of the waggle run was like a clock hand, slowly rotating as the day passed. This last observation meant that the vector of the waggle run did not simply point, in some simple referential way, to the food source. Rather, it seemed that the waggle run indicated the direction of the food source with respect to some external, moving, point of reference. Of course, in nature, there is only one predictable moving point of reference: the sun.

Von Frisch thus formulated the hypothesis that a dancing bee indicates the direction of a food source that she has found creating an angle between her waggle run and the vertical that, outside, matched the angle between the food source and the azimuth position of the sun. Using the same techniques that he had already invented, von Frisch confirmed the hypothesis. Bees use the convention that up, on the hive surface, corresponds to the position of the sun. A dance with a waggle run that is 30 degrees to the left of the vertical means that the food source is currently 30 degrees to the left of the sun. Further, von Frisch showed that the length of the waggle run corresponds to the distance between the hive and the food source. When a food source is close to the hive, within about 50 meters, the dance does not employ a waggle run. Von Frisch referred to these as round dances. The round dance simply indicates that there is food close by. For food sources beyond 50 meters, the bees begin to indicate a sun-compass direction with the waggle dance, and the waggle run becomes longer as the distance to the food source increases. The dance is a miniaturized reenactment of the forager's flight out to the food source. During the waggle run, the dancer even simulates flight, by elevating her wings slightly and vibrating them. Finally, von Frisch proved that the bees do not need to see the sun to give or receive correct directions. All they need is a patch of blue sky. That is because, like most insects, bees perceive the pattern of polarized light in the sky, and this pattern has a consistent orientation with respect to the position of the sun.

Long Trips

Most of us would be happy to receive the frequent-flyer miles racked-up by an Arctic Tern each year. These small (110 gram) gull-like birds feed at sea, plunge-diving for fish. They nest and rear their young in the Arctic summer, then fly the length of the Atlantic to spend the northern hemisphere winter in the Antarctic summer.

Figure 7.2. Arctic Terns. Photograph by Greg Gillson

Recently, researchers attached advanced lightweight geo-locating devices to several birds, and were able to show the actual migration routes. The round-trip distance flown by 11 birds that the researchers instrumented was 37,000 to 51,000 miles[56]. The researchers pointed out that, because Arctic Terns may live for 30 years, an individual's lifetime distance flown in migration is about equal to three roundtrips to the Moon.

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[56] Egevang, C., Stenhouse, I.J., Phillips, R.A., Petersen, A., Fox, J.W. & Silk, J.R.D. 2010. Tracking of Arctic terns Sterna paradisaea reveals longest animal migration. *Proceedings of the National Academy of Sciences of the United States of America* 107, 2078-2081.

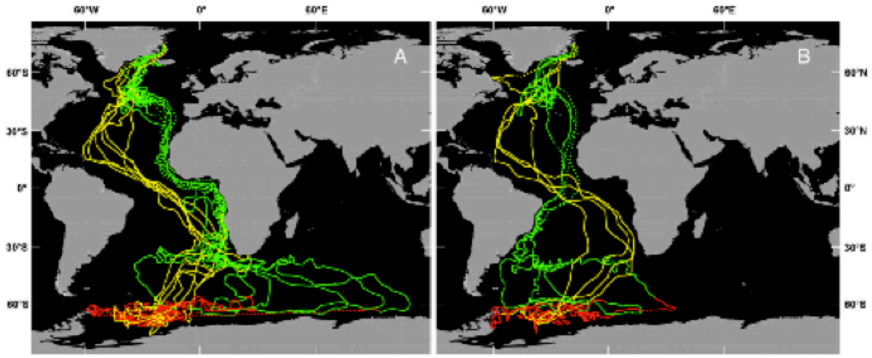

Figure 7.3. Migration routes of 11 arctic terns. Green indicates the fall route, red the wintering area, and yellow the spring return route.

This kind of flight performance depends on the ability of the terns to find and use favorable winds, and it also requires a fully functioning navigation system. If you are flying over those sorts of enormous distances, you can't afford to get off course. Therefore, you can't rely on approximate navigation that is backed up by landmarks. Although Arctic Terns represent the extreme, they are not unique. Individuals of many bird species migrate hundreds to thousands of miles every years between nesting habitat in the Northern Hemisphere and wintering habitat in or close to the Southern Hemisphere. How do they navigate with such accuracy?

A.C. Perdeck, a colleague of Tinbergen, performed a key study that set the agenda for this field of research[57]. Perdeck worked with starlings, a native Eurasian species. The population from which Perdeck sampled breeds in northern Holland, Germany, Poland, and

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[57] Perdeck, A.C. 1958. Two types of orientation in migrating starlings, *Sturnus vulgalis* L., and chaffinches, *Fringilla coelebs* L., as revealed by displacement experiments. Ardea 46, 1-37.

southern Scandinavia, and in fall migrates in huge flocks, southwest along the border of the North Sea to southern Holland, Belgium, France, England, and Ireland. For ten years, from 1948 to 1958, Perdeck and his colleagues captured starlings during migration in the vicinity of The Hague, banded them, placed them in covered cages, flew them by airplane to Switzerland, and released them. They then made a prodigious effort to recapture birds. Perdeck worked in an era before lightweight geo-locating devices existed and before the pressure to publish precluded waiting on a result until there is something significant to write about. Because the chance of recovering a released bird is small, Perdeck and coworkers continued the study for ten years, until they had caught and released 11,247 birds and recovered 354 of these. With this sample, Perdeck had something significant to report.

The clear result that Perdeck obtained was that the direction that a starling, captured in Holland and released in Switzerland, flew depended on whether it had made the migratory trip before in its life. Young of the year, that were migrating for the first time, continued to fly to the Southwest (their heading when nabbed in Holland) from Switzerland. Adults, however, flew to the Northwest, a direction appropriate to get to the migratory destination.

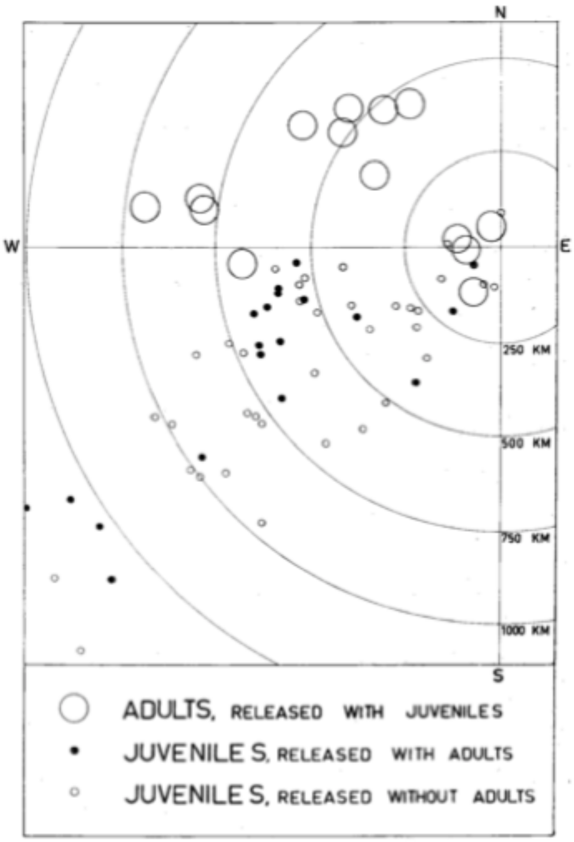

Figure 7. 4. One of Perdeck's original figures, showing different orientation directions of adults and juveniles when released in Switzerland

This result showed that the birds have two distinct navigation systems. The first, shown by the naive young, is the ability to fly in a fixed compass direction. Juvenile starlings are programmed to fly to the Southwest, and they continue to do so even when displaced. The adults, in contrast, had access to another navigation system. They seemed to know, in some sense, where they were on the globe with respect to their migratory destination, and they took up the appropriate compass heading to get there. Juvenile birds have a compass. Adults have a compass and they also have a map.

Subsequent work on birds followed and supported the conclusion, established by Perdeck, that there are two separate navigation systems, the compass sense, and the map sense. Of these two, the compass sense has proved far more amenable to experimental study. The map sense remains more mysterious. One domestic variety of the rock dove, the homing pigeon, quickly became the chosen experimental subject for study of the compass sense. Homing pigeons are tremendously useful because they will fly home when they have been displaced, and they will do so repeatedly. With a homing pigeon, the researcher does not need to wait for the subject to come into migratory condition and to make one its two annual trips.

Earlier research on the directionality of migratory restlessness in individuals of migrating species that were held in cages suggested that birds might use the sun as a source of compass information. A caged individual in migratory condition shows *Zugunruhe*, a nearly constant fluttering, hopping and flapping against the cage wall in the direction that it would move if it could. When the apparent position of the sun was changed for these birds, the orientation of their *Zugunruhe* changed. Starting with this lead, the homing pigeon researchers produced conclusive proof for a sun compass.

The proof came from clever experiments, the first of which performed by Klaus Schmidt-Koenig of the Max Planck Institute for Behavioral Physiology in the late 1950s[58]. Subsequently, many other revealing experiments took place at Cornell University, under

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[58] Schmidt-Koenig, K. 1960. The sun azimuth compass: one factor in the orientation of homing pigeons. *Science* 131: 826-828

the direction of Charles Walcott and William Keeton[59]. The key experiments involved clock-shifting, meaning that the pigeons were put on an altered light-dark cycle. The light cycle is important because the sun is useful as a cue to navigate in a fixed compass direction only when its position is used in conjunction with a clock. For example, suppose that you are in the Northern Hemisphere and that you want to fly due South. In the early morning, the sun should be on your left, at noon, straight ahead, and in late afternoon, on your right. You can't use the sun to maintain a fixed heading unless you have a clock. So, the researchers reasoned, if the birds use the sun and an internal clock to set direction, then resetting the internal clock should cause the compass heading to change. This is exactly what the clock-shifting experiments demonstrated. For example, we clock-shift a group of pigeons six hours early: they are kept indoors, where the lights come on at midnight and go off at noon. We keep the birds on this schedule for a week or so. Then, on the day of the experiment, we place the birds in covered boxes, transport them 100 km to the South, and release them, one at a time, at 6 a.m. Observers with binoculars stand on elevated towers. Each bird first flies in rough circles for a minute of two, seemingly getting its bearings, and then it flies off in a straight line. The observer watches with binoculars until the bird passes out of sight over the horizon, and then records the compass direction of that final sighting; this is called the vanishing bearing. The vanishing bearing is considered to be the best estimator of the direction in which the bird intends to fly. Now, if our clock-shifted bird has an unimpaired map sense, and knows that home lies to the North, in which direction should it fly? To the clock-shifted bird, 6 a.m. is its subjective noon: the lights have already been on for 6 hours. At noon, the sun is in the South. Our clock-shifted bird, if it is using the sun's position to

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[59] Walcott, C. 2005. Multi-modal orientation cues in homing pigeons. *Integrative and Comparative Biology* 45, 574-581, is a great historical account of this work.

compute where north is, should fly directly away from the sun, or due west. On most testing days, this is exactly what the birds did.

Magnetic Compass

Sometimes, the clock-shifting experiments did not work. The birds flew straight home, giving no indication that their clocks were off. Researchers eventually realized that these results occurred only on cloudy days, when the birds could not see the sun. Thus, it seemed that the birds had some kind of backup navigation system, not dependent on the sun. Researchers proposed that the backup system must be based on the other obvious directional cue in the environment, the Earth's magnetic field.

How does one discern whether a bird's compass depends on the ability to detect the Earth's magnetic field? One removes some feathers from the bird's back and glues on a bar magnet. As a control, one can glue on a brass bar of equal weight. Somewhat more precise control can be arranged by fitting the pigeon with a harness that carries a radio-controlled electromagnet. Both sorts of experiments worked. They showed that, on cloudy days when birds could not see the sun or blue sky, altering the magnetic field around the bird's head disrupted its homeward migration. The same treatments performed on sunny days had little effect. If birds wearing magnets on cloudy days began flying in the wrong direction and then the clouds parted, the birds immediately reversed course, flying back across the release point toward home. Thus, pigeons and other birds have two compass systems. The first is a sun azimuth based system that works in conjunction with an internal clock. Young birds learn to calibrate the motion of the sun with their own clocks during a sensitive period in development, when they must fly with a view of the sun to accomplish the calibration. Birds appear to give priority to the sun compass, but if the sun compass is not available, then they rely on a magnetic compass.

How do birds extract useful information about compass direction from the magnetic field of the Earth? One obvious possibility is that they have the equivalent of the compasses that we use and thus are sensitive to polarity. The other, more arcane, possibility is that birds are able to detect magnetic inclination, the angle between field magnetic vectors and the Earth's surface. As one moves from the equator toward the pole, this angle changes, from zero at the equator where the field vectors are parallel to the Earth's surface, to 90 at the pole, where the vectors point inward to the pole. Thus, the average angular change is about 0.009 degrees per kilometer. A detector that indicated the direction toward the pole would need to be very sensitive. However, as we have already seen, from the example of shark electroreception in Chapter 2, animals may evolve extraordinarily sensitive sensory capabilities when there is a survival advantage at stake. Recent work has proved that the magnetic compass of birds is an inclination detector. The inclination sense simply discriminates between poleward (inclination vectors pointing downward) and anti-poleward (inclination vectors pointing upward), and thus is uninformative near the equator, where the magnetic field vectors are parallel to the Earth's surface. Nevertheless, experiments in which birds are exposed to manipulated magnetic fields show clearly that a bird that intends to fly North will orient to the South when magnetic north polarity is unchanged but magnetic inclination is flipped.[60] The best evidence to date is that birds sense magnetic inclination with their eyes. In effect, they see the direction toward the pole.[61]

Stars

Many bird species that migrate away from the Northern Hemisphere in fall do all of their long-distance flying at night. The birds rest and eat during the day, then start each leg of the migratory trip at dusk. For a little while, afterglow on the western horizon provides some compass information, but soon the sky is dark, and there are no cues to indicate the position of the sun. Also, the magnetic compass, which is light-based, is unavailable. To maintain a steady southbound heading, night flying migrants use yet another navigational sense: the ability to compute compass direction from the pattern of stars in the night sky. The first conclusive proof for star compass orientation came from the Ph.D. dissertation research of Stephen Emlen, conducted at the University of Michigan in the 1960s. Emlen worked on Indigo Buntings, a North American species that breeds in the eastern United States and migrates at night mainly to Mexico and Central America.

Emlen held captive buntings until they were in migratory condition, and then monitored the directionality of *Zugunruhe* of individuals under a simulated night sky in a planetarium. In the planetarium, each bird was placed in a funnel-like apparatus that gave it a view of

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[60] Wiltschko, R. & Wiltschko, W. 2009. Avian Navigation. *The Auk* 126, 717-743.

[61] Ritz, T., Adem, S. & Schulten, K. 2000. A model for photoreceptor-based magnetoreception in birds. *Biophysical Journal* 78, 707-718.

the simulated sky overhead, but of nothing to the side. The design of these funnels was clever:

> "The apparatus consists of a blotting paper funnel, an ink pad base, and a screen top (Figures 1 and 2). In the unit illustrated the walls are formed from a white desk blotter which is cut, rolled, and stapled in the shape of a funnel with a slope of 45 degrees, a top diameter of 35 cm, and a bottom diameter of 10 cm. This funnel rests on the rim of a two quart aluminum pudding pan to the bottom of which is glued a thin sponge sheet kept moist with black printers' ink. A square of one-half inch mesh hardware cloth, folded down at the four corners to hold it in position, caps the funnel...The complete cost of such a unit is about 65 cents, and replacement blotters for successive tests can be obtained in bulk for 4 cents each.
>
> The size of the funnel can be varied in accordance with the size of the bird to be tested, but we obtained good results with our unit for birds ranging in size from kinglets to thrushes.
>
> A bird placed inside one of these orientation funnels finds itself standing on the ink pad surrounded by outwardly sloping walls of white blotting paper; the sky is visible overhead and trees and other objects comprising the horizon are screened from view. Thus placed, a bird (for example, a White-throated Sparrow, *Zonotrichia albicollis,* White-crowned Sparrow, *Z. leucophrys*, or Indigo Bunting, *Passerina cyanea*) in migratory condition stands in one place or turns slowly in a circle, its bill tilted upwards, its wings partially spread and quivering rapidly--posture and movements closely resembling those described as *Zugunruhe* behavior for sylviids by Sauer (1957) and Bobolinks (*Dolichonyx oryzivorus*) by Hamilton (1962b). At frequent intervals the bird hops forward onto the sloping white paper, only to slide back and continues

> its pointing and quivering. Such hops from an ink pad leave clear black prints on the blotting paper and it is the accumulation of these inked footprints which produces the orientation record of the bird's activity."[62], pp 361-362.

With each bird recording the direction in which is motivated to move, many birds could be tested simultaneously under the planetarium night sky. The advantage of a planetarium is that you can make the stars obey your commands. For example, you can remove selected stars, entire constellations, or larger patches of the night sky. You can change the apparent time of night, and you can control whether the stars continue in their normal nighttime circular path around the pole star. Finally, if you are devilishly clever, you will decide to make all the stars rotate, not around the North star, but around another star. Emlen did all of these things, and proved that: 1) indigo buntings in fall migratory condition try to move south as indicated by the planetarium sky, 2) indigo buntings in spring migratory condition try to move north as indicated by the planetarium sky, 3) conjunction between the time indicated by the bird's internal clock and the time indicated by the planetarium sky was unimportant, 4) no particular stars or groups of stars were critical; any few stars somewhere in the circumpolar 35 degrees were sufficient to allow the birds to orient correctly.[63] Thus, it seemed that the birds knew, in some way, the spatial relationship between any pair or group of stars and the pole star. For example, a line that intersects the two pointer stars in the Big Dipper always extends to the pole star. Emlen proposed that the birds needed to learn how to view the sky. To test this hypothesis, he captured newly

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[62] Emlen, S.T. & Emlen, J.T. 1966. A technique for recording migratory orientation of captive birds. *The Auk* 83, 361-367.

[63] Emlen, S.T. 1967. Migratory orientation in the indigo bunting, *Passerina cyenea*. Part II: Mechanism of celestial orientation. *The Auk* 84, 463-489.

hatched indigo buntings, brought them to the laboratory, and divided them into three experimental groups. Group One birds lived in a room where the lights came on and went off to reflect normal day length, but Emlen stretched a diffusing plastic sheet below the lights, so that the birds never saw a point source of light. Emlen moved Group Two birds to a planetarium every night and provided them with a view of a normally rotating night sky. Emlen moved Group Three birds to a planetarium every night and provided them with an altered view of the night sky, in which all the stars rotated, not around the pole star, but around Betelgeuse, a bright star in the constellation Orion. The three groups were then tested under a normal night sky in the planetarium. Group One birds showed *zugunruhe,* but no directional preference; their orientation was not different from random orientation. Group Two birds showed significant orientation toward south as indicated by the planetarium sky; they oriented away from the pole star. Group Three birds also showed directed, nonrandom orientation, but they oriented in the direction away from Betelgeuse. Thus, Emlen proved that indigo buntings must learn how star patterns indicate direction, and that they do so by observing, when they are young, the axis around which all the nighttime stars appear to rotate.[64]

Magnetic Map?

In a typical homing experiment, in which a pigeon is transported in a covered cage in an automobile and then released, perhaps 100 km from home, the bird shows little hesitation about where to go. The bird flies in rough circles for a minute or less and then heads away

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[64] Emlen, S.T. 1970. Celestial rotation: its importance in the development of migratory orientation. Science 170, 1198-1201.

along a straight line path. The direction that the bird chooses may be incorrect (because the bird was clock-shifted), but there is little apparent indecision in choosing that direction. In other words, the bird obviously "knows," in some sense, where it is on the map with respect to home. If experimenters have not disrupted the bird's compass, then it chooses the correct heading toward home. Experiments in which the compass is disrupted by clock shifting could only work if the subjects had unimpaired map information. A bird is clock shifted 6 hours early and is released south of home at dawn. The bird flies west, away from the sun, because it intends to fly north. The clock-shifted orientation shows quite clearly that the compass sense is independent of the map sense.

How does the map sense work? At present, the short answer is that we don't know, but that the sense seems to be based on detection of some aspects of the Earth's magnetic field. Researchers have proposed that an effective map sense must be based on a bi-coordinate system that is analogous in some way to the human bi-coordinate system of latitude and longitude. They have pointed out that a bi-coordinate system of sorts is available to animals that can detect magnetic inclination and magnetic field intensity. When isoclines of these two aspects of the Earth's magnetic field are plotted, they form a rough bi-coordinate grid. Thus, across large areas of the Earth's surface, location can be represented by the local readings of magnetic field inclination and intensity.

Some of the best evidence for the magnetic map hypothesis comes from an innovative study done by Kenneth Lohmann and colleagues at the University of North Carolina.[65] The

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[65] Lohmann, K.J., Cain, S.D., Dodge, S.A. & Lohmann, C.M.F. 2001. Regional magnetic fields as navigational markers for sea turtles. *Science* 294, 364-366.

Lohmann group has worked on the orientation of sea turtles, and especially Loggerhead turtles, for many years. After it hatches in the warm sand of a Florida beach, a baby loggerhead turtle runs, as best as a reptile with flippers for legs can run, down to the sea, and begins to swim east. If it is not picked off the beach or out of the shallows by the gulls that hover overhead for this breakfast opportunity, it continues to swim east until it meets the Gulf Stream, the northeast-bound part of a vast circular current called the North Atlantic Gyre. For the next few years, the turtle feeds and grows within the Gyre. The turtle needs to remain within the Gyre's latitudinal limits. If the turtle makes a mistake and strays north of the Gyre, it will die in the rapidly cooling water. A turtle that strays to the South risks being carried into the South Atlantic current system, which would carry it far from the habitat to which it is adapted, and from the beaches to which it will home to lay eggs.

The Lohmann group decided to test the hypothesis that young turtles could detect magnetic field inclinations and intensities that indicated that they were in danger of leaving the North Atlantic Gyre. To test this hypothesis, they outfitted hatching turtles, that had never been in the ocean, with harnesses that held the turtles in place, but allowed them to orient and swim toward any direction inside a circular tank in the lab. Next, the researchers used magnetic coils that surrounded the tank to create field inclinations and intensities that were characteristic of one of three widely spaced locations at the edge of the North Atlantic Gyre. The first simulated location was just offshore from the coast of north Florida. The second was off the coast of Portugal, where the northbound Gulf Stream splits from the Gyre current that swings south, past the coast of Africa. The third was at the southern side of the Gyre, about midway between west Africa and Brazil. The results strongly suggested that the young turtles in effect knew where they were. In response to a magnetic field that indicated that they were off the coast of north Florida, the turtles swam to the Southeast. In response to a magnetic field that indicated that they were at the north edge of the Gyre, near Portugal, the turtles swam south. In response to a magnetic field that placed them at the southern edge of the Gyre, the turtles swam northwest. Thus, loggerhead turtles, when they enter the ocean for the first time, come equipped with the ability to detect magnetic field inclination and intensity, and to use this information to swim in a direction that will keep them within appropriate habitat.

More recently, several groups of researchers have manipulated the magnetic fields around birds captured during migration. Birds that are given magnetic information indicating that they are at the start of a long flight across water or desert eat more, and put on more fat than control bird that are given magnetic information indicating their true location. In one of the most amusing of these studies, researchers captured juvenile wheatears in Sweden, and subjected the experimental group to magnetic information indicating that they were in the Atlantic Ocean south of Greenland and, over the next few days, were moving due south. The control birds were given magnetic information that indicated that they were on a normal migratory path to west Africa. The experimental birds ate more, and put on fat.[66] The magnetic map information told them that they were in the middle of a long ocean

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[66] Boström, J.E., Fransson, T., Henshaw, I., Jakobsson, S., Kullberg, C. & Åkesson, S. 2010. Autumn migratory fueling: a response to simulated magnetic displacements in juvenile wheatears, *Oenanthe oenanthe*. Behavioral Ecology and Sociobiology 64, 1725-1734.

flight, and they ate accordingly, apparently not too confused by the wooden shed they were living in, the mealworms provided, and the absence of any kind of ocean view.

Chapter Eight

Genetics

The blackcap (Sylvia atricapilla) is a common, widespread Eurasian warbler. In fall, individuals that spent the summer in Europe migrate to North Africa. A bird migrating to Morocco from France obviously has a much shorter trip than a bird migrating from Finland. Researchers captured nestlings from four populations: Finland, Germany, France, and the Canary Islands. They raised the birds in captivity in Germany under uniform conditions. In fall, the researchers monitored the duration of *zugunruhe* of the birds, and found that individuals from the Finnish population had the longest durations, followed by the German, the French, and finally by the Canary Island Birds.[67] These results suggested that the birds of these four populations differed genetically in the programmed duration of migration. To provide further proof of this hypothesis, the researchers mated German birds to Canary Island birds, and then recorded the duration of *zugunruhe* of the hybrid offspring. The hybrids, with a German father and a Canary Island mother or vice versa, had *zugunruhe* durations that were midway between the parental values.

Another study on the same species looked at the preferred compass heading shown in *zugunruhe*. Blackcaps from western Europe migrate by flying southwest until they reach the Strait of Gibraltar. Then they turn south and make the short over-water crossing to Africa. There, the birds will winter in Morocco or in west Africa below the Sahara. All blackcaps in western Europe make this trip, but, in populations that are east of a dividing

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[67] Berthold, P & Querner, U. 1981.Genetic basis of migratory behavior in European warblers. *Science*, 212, 77-79.

line that lies somewhere in Austria, there is a shift in the migration path. The eastern European birds fly southeast to the Dardanelles and across Turkey before turning south to fly along the eastern coast of the Mediterranean Sea, across the Red Sea to east Africa at a level with or below the Horn. In other words, European blackcaps avoid flying directly across the Mediterranean Sea - they go around it, either to the West or to the East. In a study design that was similar to that used to look at the duration of *zugunruhe*, researchers captured nestlings from western and eastern populations, raised them in the laboratory under uniform conditions and then, in the birds' first fall, recorded the directional preference of *zugunruhe*. Birds from the western populations showed a clear preference to move southwest, and birds from the eastern populations a clear preference to move southeast. Hybrid offspring from parents of the two populations had preferred migration directions that were almost due south, intermediate between the parental values.[68]

These results, on duration and direction of *zugunruhe*, are typical of the results one gets when one creates hybrids from two distinct parental lines that show genetically based differences in behavior. The behavior of the hybrid offspring is usually intermediate. It is essentially an average of the values of the mother and the father. From these findings, we can conclude two things about the genetic control of behavior. First, genetic differences among individuals contribute significantly to the total variation in behavior among individuals. Second, most measurable aspects of behavior, such as the duration or orientation of *zugunruhe*, are controlled by many genes.

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[68] Helbig, A.J. 1991. Inheritance of migratory direction in a bird species: a cross-breeding experiment with SE- and SW-migrating blackcaps (*Sylvia atricapilla*). *Behavioral Ecology and Sociobiology* 28, 9-12.

If a behavioral phenotype is determined by only one or two genes, then hybrid offspring would not show continuous variation: they would fall into discrete bins. For example, suppose that the duration of *zugunruhe* is controlled by variation in a single gene. Each individual bird, like most animals, is diploid. Each of its cells contains two copies of each chromosome and thus two copies of each gene. A chromosome is a single long molecule of DNA that comprises hundreds to thousands of genes. Genetic variation exists because a gene copy may come in two or several different forms. In other words, the sequence of nucleotides that constitute the gene can vary somewhat. This variation is created by errors in DNA copying when eggs or sperm are made. These copying errors are called mutations. For the purposes of our illustration, let's assume that the *zugunruhe* gene comes in two forms, which we will designate as A and a. Because each individual has two copies of each gene, an individual's genotype may be AA, Aa, or aa. Now assume that a bird with a genotype of AA has a *zugunruhe* duration of 8 days, that a bird with an Aa genotype a duration of 6 days, and a bird with an aa genotype a duration of 4 days. When a male bird of genotype Aa mates with a female of genotype Aa, what are the possible genotypes of their offspring? A sperm contains only one copy of each chromosome and so does an egg. When they join, the sperm and egg will create a new diploid (two copies of each chromosome) cell that will start dividing and developing into a new bird. We keep track of possible genotypes of the baby birds with a mating table, shown below, that shows the possible sperm and egg combinations. Possible sperm are shown in the rows, and possible eggs in the columns. The four possible offspring genotypes are shown in the cell entries.

		Egg Types	
		A	**a**
Sperm Types	**A**	AA	Aa
	a	Aa	aa

Table 8.1 - A mating table, showing the offspring genotypes that are produced by mating between a father with genotype Aa and mother with genotype Aa.

One-fourth of the offspring will be genotype AA, with *zugunruhe* durations of 8 days, one-half will be genotype Aa, with *zugunruhe* durations of 6 days, and the remaining one-fourth will be genotype aa, with *zugunruhe* durations of 4 days. There are no intermediates, with zugunruhe durations of 7 days, or 5 days. It was by following pedigrees and observing proportions like these in garden plants that Gregor Mendel deduced the existence of genes.

Phenotypes of individuals fall into discrete bins when a single gene controls the trait being measured. What happens if two genes are in control? If the second gene can also take one of two alternate forms (we call the alternate forms of genes alleles), which we will designate as B and b, how many possible genotypes are there? There are 9, as shown in the following table. The table also shows hypothetical values for *zugunruhe* duration of each genotype.

		B Genotype		
		BB	**Bb**	**bb**
A Genotype	**AA**	AABB 10	AABb 9	AAbb 8
	Aa	AaBB 8	AaBb 7	Aabb 6
	aa	aaBB 6	aaBb 5	aabb 4

Table 8.2 - When two genes, each with two alleles, control a trait, there are 9 possible genotypes. Values below each genotype show hypothetical *zugunruhe* durations.

In what proportions will these genotypes appear? We figure this out by constructing a mating table, as we did to get genotype frequencies for a single gene. We show the possible male gametes in the rows and the possible female gametes in the columns:

		Egg Types			
		AB	**Ab**	**aB**	**ab**
Sperm Types	**AB**	AABB	AABb	AaBB	AaBb
	Ab	AABb	AAbb	AaBb	Aabb
	aB	AaBB	AaBb	aaBB	aaBb
	ab	AaBb	Aabb	aaBb	aabb

Table 8.3 - A mating table, showing the offspring genotypes that are produced when two genes, each with two alleles, control a trait.

Now we count the genotypes in Table 8.3, and we get the following result:

Genotype	Number	*Zugunruhe* Duration
AABB	1	10
AABb	2	9
AAbb	1	8
AaBB	2	8
AaBb	4	7
Aabb	2	6
aaBB	1	6
aaBb	2	5
aabb	1	4

Table 8.4 - When two genes, each with two alleles, control the duration of *zugunruhe*, genotypes appear in numbers as shown. *Zugunruhe* durations are transcribed from Table 8.2.

We can then view the expected spread of *zugunruhe* durations with a frequency histogram, which is a plot with trait values on the X-axis and the number of observations of that value on the Y-axis:

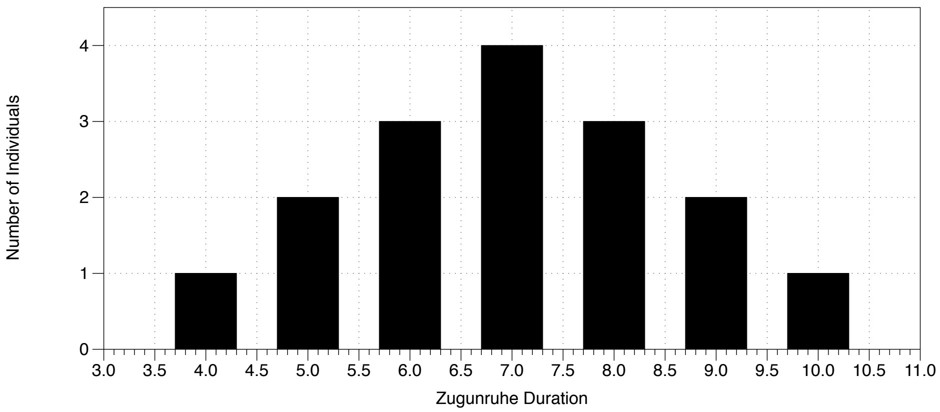

Figure 8.1 - Frequency distribution of *zugunruhe* durations when two genes, each with two alleles, control the trait.

If we add a third gene, also with two alleles, now there are 27 possible genotypes. If ten genes, each with two alleles, control the trait, then we have 59,049 possible genotypes. Now there are so many bins that all the spaces between bins that exist in Figure 8.1 become filled in, and we can replace the discrete frequency distribution with a continuous one: the familiar bell curve, or Gaussian Distribution, that describes the array of values of many things in nature. Most behavioral traits, like *zugunruhe* duration, when measured in many individuals, have this kind of frequency distribution. This tells us that most behavioral traits are controlled by multiple genes.

This should not be too surprising, because behavior is the result of action potentials that travel along motor nerves to muscles. The brains that make the decisions about which muscles to contract from moment to moment are complex organs. Brains and other organs are built by the developmental process in which a single fertilized egg divides, and its daughter cells divide, and those granddaughter cell divide, and so on until there are enough cells to make up the blocks of primordia that will become guts, muscles, bone, skin, nervous system. These incipient tissues participate in an unfolding developmental program to take on species-specific structure and function. The developmental program is complex, and is regulated by the closely timed and coordinated expression of hundreds of genes. Thus, it is generally unlikely that a connection between a single gene and a behavioral outcome could be found. Genes do not cause behavior. Genes build brains, and brains cause behavior.

Even though most behavioral acts emerge from the expression of many genes, we can still study how these traits are inherited, and we can form estimates of the rate at which behavioral change will occur when there are new selection pressures that are caused by changes in the natural environment. Traits that are controlled by many genes, and which therefore vary continuously (no discrete bins) are called quantitative traits, and the study of the genetics of such traits is called quantitative genetics. Quantitative genetics relies heavily on two statistics that one can calculate from continuously varying data: the mean and the variance. The mean, or average, is familiar to many people. We sum all the individual values in our sample and divide that sum by the number of individuals that we sampled. For example, to calculate the mean from the data shown in Table 8.4 and Figure 8.1 we take (1 x 4) + (2 x 5) + (3 x 6) + (4 x 7) + (3 x 8) + (2 x 9) + (1 x 10) = 112 and divide this result by the number of individuals (16) to get the mean of 7. The mean calculated this way is called the arithmetic mean, and it is often an accurate descriptor of the central tendency in a group of data, as it is when we look as Figure 8.1. Calculation of an estimate of the variance is only a bit more complicated. From a discrete sample, the variance is defined as the average squared difference from the mean. To calculate the variance for the data shown in Table 8.4 and Figure 8.1, we take $1 \times (4-7)^2 + 2 \times (5-7)^2 + 3 \times (6-7)^2 + 4 \times (7-7)^2 + 3 \times (8-7)^2 + 2 \times (9-7)^2 + 1 \times (10-7)^2 = 40$, and divide by the number of samples (16) to get 2.5. The data shown in Table 8.4 and Figure 8.1 have a mean of 7 and a variance of 2.5. Two different samples could have the same mean but different variances. The variance describes the degree of spread around the mean. A large variance means that there are many values far from the mean and a small variance means that most values are clustered close to the mean.

When we measure a behavioral variable in a sample of individuals, the variance that we calculate is called Total, or Phenotypic variance. The quantitative genetic approach considers phenotypic variance to be a sum that is composed of two main parts. These are environmental variance and genetic variance. Suppose, for example, we measure IQ in a thousand humans. The distribution of IQ values will be Gaussian (a bell curve). A small number of individuals will have very low IQ scores and an equally small number will have very high IQ scores. Most individuals will cluster around the mean IQ score. Now, what causes the variation in IQ score? On one hand, we could assert that all the variation must be due to the environment, including effects such as the mother's nutrition during gestation, postnatal nutrition, exposure to toxins, illness, parental involvement in education, and so on. Alternatively, we could assert that all the variation is due to variation in individual genotype. For IQ, as is so for nearly all behavioral traits, the answer is that both environment and genotype contribute to the total variation, so we write $V_P = V_E + V_G$. Total or phenotypic variance equals variance due to environmental effects plus variance due to genotype. Furthermore, geneticists know that V_G can be represented as the sum of three components. These are additive effects, V_A, dominance effects, V_D, and interactive effects, V_I. So, we write $V_G = V_A + V_D + V_I$.

To understand these separate components of genetic variance, look again at Table 8.2. The table shows that individuals with different genotypes have different *zugunruhe* durations. I made up the data in Table 8.2 in a special way to show all additive genetic variance. Notice that, anywhere in the table, the effect of replacing an a allele with an A allele is an increase of 2 days. The effect of replacing a b allele with a B allele is always an increase of 1. In Table 8.2, all the effects on phenotype are additive genetic: the effects of individual alleles simply add up. If genetic dominance existed, then, for example, the genotype AaBB (row 2, column 1) would have a value of 10, just like AABB, because only one copy of the A allele is needed to get a full effect. Interactive effects, also called epistasis effects, mean that the effect of one allele depends on the genotype for another gene. For example, note that all the values in row 2 (Aa genotypes) increase by 2 in row 1 (AA genotypes) the effect of replacing a with A is always an increase of 2. To illustrate an interactive effect, change the value in row 1 column 3 to a 6. Now, if we compare row 2, column 3 to row 1, column 3, the effect of replacing an a allele with an A allele is no longer 2, it is zero. If the B genotype is BB, or Bb, the effect of replacing a with A is still 2, but if the B genotype is bb, then this A effect disappears. The effect of the A genotype was dependent on the B genotype. That is an interactive effect.

Of these three genetic effects, additive, dominance, and interactive, quantitative geneticists tend to be most interested in additive effects. That is because additive effects are responsible for the resemblance between parents and offspring. Let's go back to table 8.2, which, remember, illustrates all additive effects. Now, let's create a few matings between parents with different *zugunruhe* values and compare the mid-parent value (average of the two parents) to the offspring value. I have done this in Table 8.5.

MALE PARENT		FEMALE PARENT		MID-PARENT ZUGUNRUHE	OFFSPRING	
Genotype	Zugunruhe	Genotype	Zugunruhe		Genotype	Zugunruhe
aaBb	5	aabb	4	(5+4)/2 = 4.5	aaBb aabb	5 4 mean = 4.5
AAbb	8	aabb	4	(8+4)/2 = 6	Aabb	6
AABB	10	aabb	4	(10+4)/2 = 7	AaBb	7
AABB	10	aaBB	6	(10+6)/2 = 8	AaBB	8

Table 8.5 - From Table 8.2, we take values for parental genotypes, generate the offspring genotypes and find offspring values from the same table

Now, we plot the offspring values against mid-parent values to get the following:

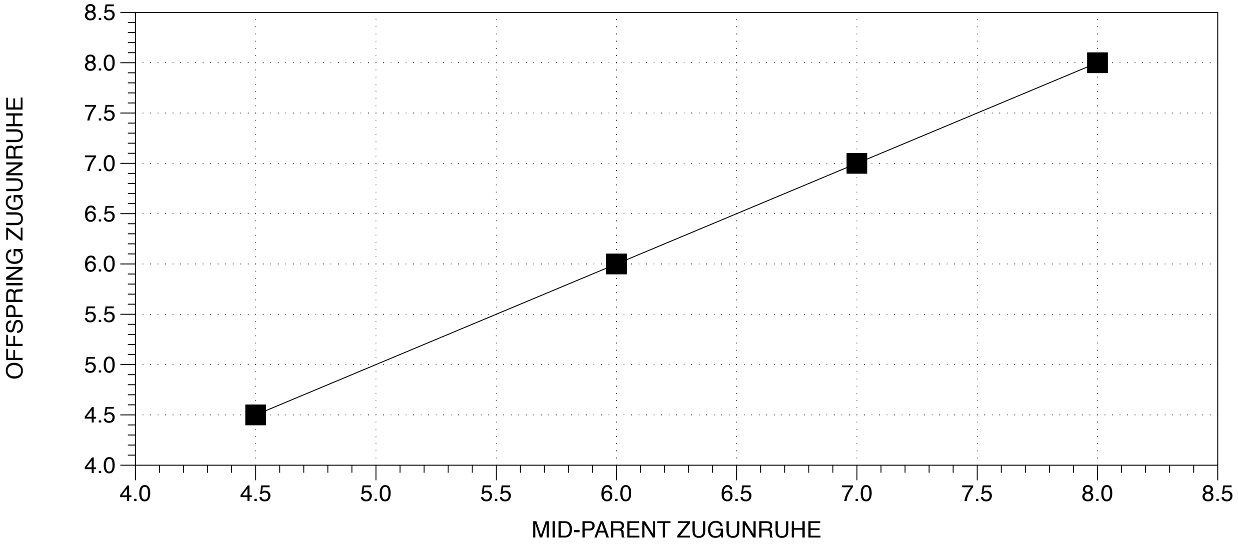

Figure 8.2 - Plot of mid-parent values against offspring values of *zugunruhe*. The data were taken from Table 8.5.

The line in Figure 8.2 is at an angle of 45 to the horizontal. It has a slope of 1, meaning that, to stay on the line, for every increase along the X-axis, we must make the same increase along the Y axis. The slope of this line is equal to an important value in quantitative genetics called heritability, and designated as h^2. In reality, when we measure mid-parent and offspring values, we don't get a set of points that fall neatly on the line as in Figure 8.2. Instead, we get scatter, as illustrated in the following figure:

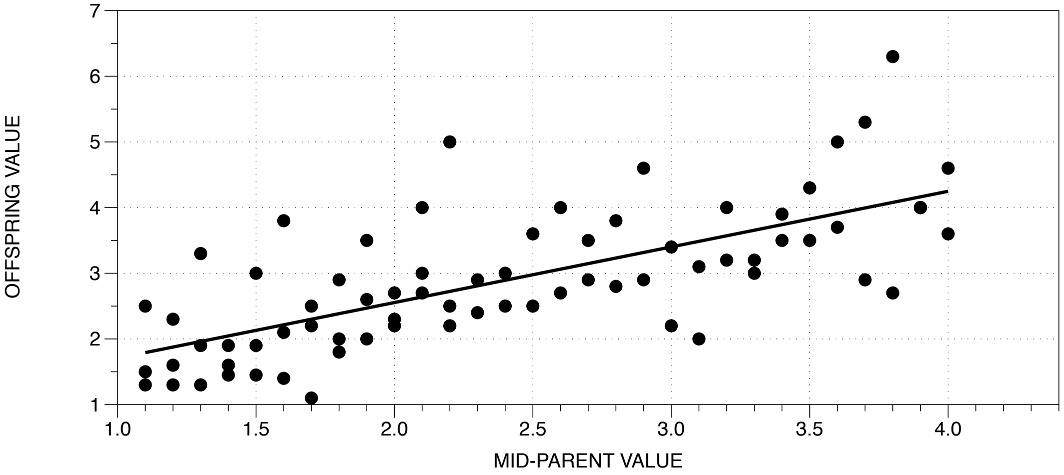

Figure 8.3 - Made-up values to show a typical plot of mid-parent values on offspring values for a behavioral trait.

The line that is drawn through the cloud of points is derived by a statistical procedure that finds the straight line that results in the minimum sum of squared differences between each point and the line. This is called a least-squares regression line, and the slope of this line is equal to the heritability. In Figure 8.3, this value is 0.85. Another way to express heritability is as a ratio. It is defined as V_A/V_P. In other words, the heritability of a trait is the proportion of total phenotypic variance that is attributable to the additive effects of alleles. Because I designed Table 8.2 to show only additive genetic effects, the mid-parent-offspring plot from the data show a slope of 1. The heritability is 1, meaning that 100% of the variance in *zugunruhe* duration is attributable to additive effects of alleles. In the relationship shown in Figure 8.3, the slope of the least-squares regression line is 0.85, so 85% of the phenotypic variance is attributable to additive effects of alleles, and the remaining 15% is attributable to some combination of environmental effects and non-additive genetic effects (V_D and V_I).

Heritabilities have been measured for hundreds of behavioral traits, including locomotion, nesting, social dominance, aggressiveness, vigilance, grouping tendency, exploratory behavior, fearfulness, sensitivity to pain, maternal solicitude, willingness to help parents raise new offspring rather than breed for oneself, social play, wheel running, and mating speed, to list a few examples. The heritabilities range from about 0.10 to 0.75, with most falling in the 0.3-0.5 range.

Because most measured behavioral traits have significant heritabilities, it should be possible to modify behavior by selective breeding, and it is. There are many examples of such modification. First, as Charles Darwin pointed out in the first chapter of The Origin of Species, many differences in behavior are apparent among the domestic varieties of animals, such as pigeons, chickens, cattle, and sheep. Darwin paid special attention to the huge variety among domestic pigeons, all of which are descendants of the wild Rock Dove. Along with a riot of sizes, shapes, colors, and plumage, the breeds of domestic pigeons also show many differences in behavior. Pigeon breeds vary in vocalizations, postures, walking gait, flying maneuvers, flight speed, and homing ability, and even the ability to fly (some breeds cannot). These differences were created by humans, who controlled the breeding of their pigeons, allowing individuals with desirable (defined by the human owners) behavioral traits to reproduce, and culling animals with undesirable behavior.

Another intriguing example may be found in the domestic sheep of North America. In western North America, domestic sheep are unusually vulnerable to coyotes. When a sheep is grasped about the neck by a coyote's jaws, it tends to go limp, as if it is saying to the coyote, "I give up: go ahead and eat me." This is odd, because a domestic sheep weighs a lot more than a coyote. If an individual struggled vigorously, it might be able to fend off a coyote attack. However, individuals don't struggle, and so the coyote enjoys an easy meal. How can this be? Certainly, the responses of individual sheep contradict the central tenant of optimality in animal behavior, that animals should be programmed to act as if they are constantly evaluating the question: "what should I be doing at this moment to maximize my lifetime fitness?"

The answer to this paradox is that the behavior of domestic sheep has been modified by the selective breeding inherent in the domestication process. In the history of domestication of sheep from a wild Eurasian species, humans have selected for an increase in the volume of wool, for changes in body conformation that yield better cuts of meat, and for feeding efficiency and growth rates. Since the start of large-scale sheep shearing, humans have selected for an immobility response when the shearer grasps the sheep and plants it on its rump between his legs. Sheep that struggled and would not hold still for shearing were not allowed to breed. In consequence, modern domestic sheep are relatively easy to shear. However, the immobility response when grasped that makes them easy to shear also makes them fail to struggle when they are grasped by a coyote.

Making Nice Foxes

In a few cases, the behavioral outcomes of the domestication process were studied more systematically. One of the most famous of these studies is the Silver Fox experiment, begun in 1959 by the Russian geneticist, Dmitry Belyaev. Belyaev wanted to replicate the process by which a wild species becomes domestic. He started a selective breeding experiment on foxes taken from an Estonian fox farm. Thus, he did not start at the precise beginning of the domestication process, because these foxes were descendants of individuals captured in the wild many generations previously. But, the foxes at the start of Belyaev's experiment were hostile and fearful toward humans. Belyaev's intent was to select on a single behavioral trait: tameness toward humans.

Each generation, researchers tested juveniles for tameness, starting at age one month, and then at one month intervals. Then, at 7-8 months of age, when individuals were sexually mature, the researchers assigned each to one of three tameness classes. A fox placed into class III flees humans, and when cornered in the cage, crouches, snarls, and snaps. A fox placed into class II can be touched, but it only tolerates the touch, and it shows no attraction to humans. A fox placed in to class I approaches the experimenter, wags its tail, and whines. In each generation, only the tamest individuals, generally less than 10% of those tested, were allowed to breed. Belyaev died in 1985, but some of his colleagues continued the selection experiment. Now, after more than 30 generations of selection and 50,000 tested individuals, the foxes have been transformed.[69] Most individuals when tested will jump into the researcher's arms and lick her face. They are affectionate, eager to please, and they compete with each other for human attention.

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[69] Trut, L., Oskina, I, & Kharlamova, A. 2009. Animal evolution during domestication: the domesticated fox as a model. *BioEssays* 31, 349-360.

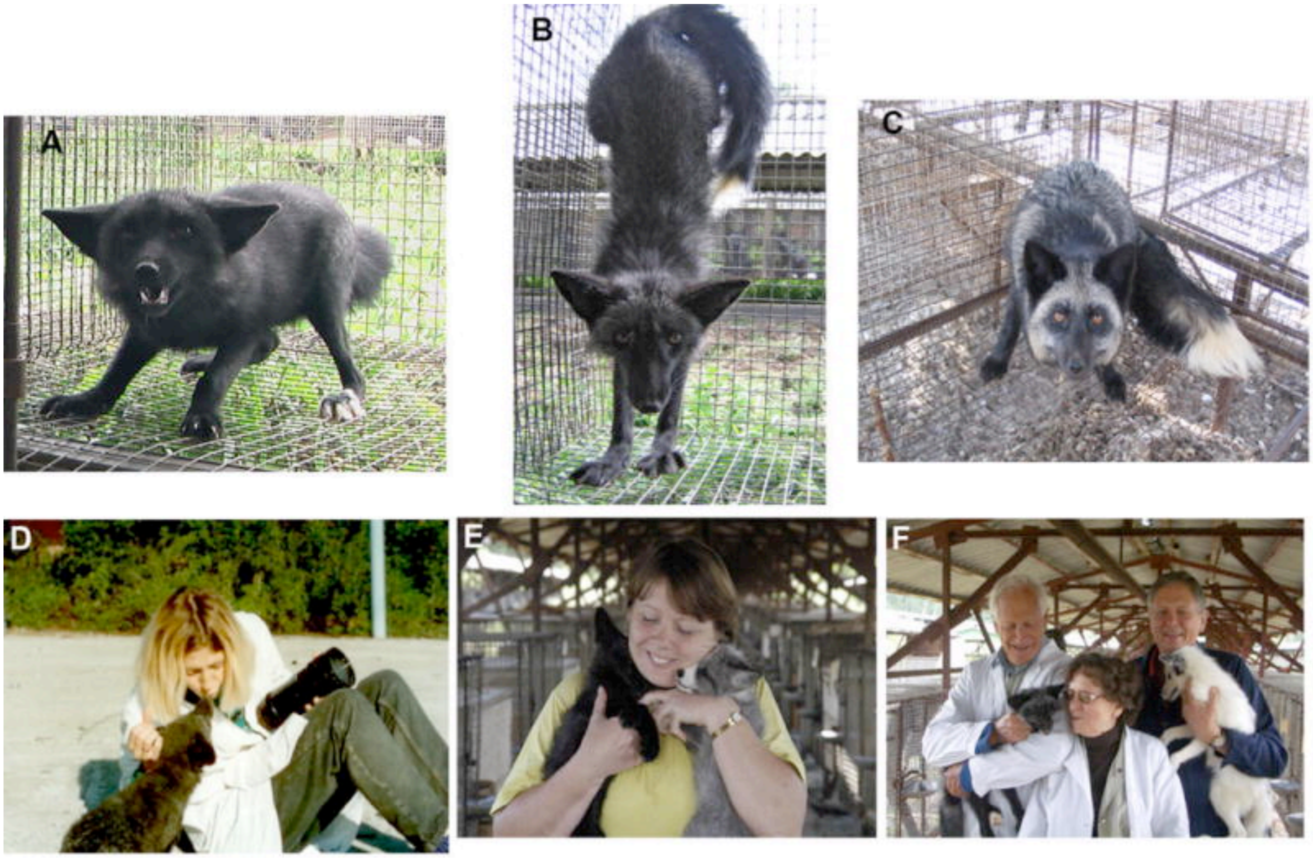

Figure 8.4. Results of the fox tameness selection study. The top row, images A, B and C show the reactions typical of wild foxes when approached by a human. The bottom row, images D, E, F show the reactions of foxes from the line selected for tameness to humans. Figure reproduced from Trut et al. 2009 (footnote 3) with permission.

In a few decades, the Belyaev experiment re-created the process, which likely took place over thousands of years, by which the wolf was transformed into the domestic dog. The Belyaev experiment achieved quicker results because the selection on a behavioral trait was rigorous, based on repeated testing of individuals, and quite severe, allowing less than 10% of individuals each generation, only the most tame of those tested, to breed. In the domestication process that led to the domestic dog, selection was much more intermittent and haphazard, and was certainly not based on the repeated, formal testing of individuals. Nevertheless, the elite foxes of the Belyaev experiment today are strikingly like domestic dogs in their affection for humans, their ability to follow human hand signals[70], their tendency for white splotches on the coat, floppy ears, curled tails, and in their delayed postnatal development, which provides for a longer period during which bonding to humans can occur, as well as for a shortened muzzle. These results provide another reminder that it is misleading to think about "genes for behavior." The genetic changes that resulted from the Belyaev selection study were those that affected the timing of development, hormones that regulate the stress response, and others not yet identified. Belyaev selected on a single behavioral trait, tameness, and in doing so caused comprehensive developmental and genetic changes that affected far more than the specific behavior that was the target of selection.

ADHD Mice

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[70] Hare, B., Plyusnina, I, Ignacio, N., Schepina, O.,Stepika, A., Wrangham, R., & Trut, L. 2005. Social cognitive evolution in captive foxes Is a correlated by-product of experimental domestication. *Current Biology*, 15, 226–230.

Another research project, involving selection on the behavior of captive animals, that rivals the silver fox experiment, is the mouse wheel running study. This work, performed by Ted Garland and many collaborators, has extended for almost twice as many generations as the fox study, and has been even more thorough in the examination of the correlated changes that come along with selection on a behavioral trait. The primary logistical issue in any attempt to practice selection on a behavioral trait is that the trait must be measured. Measurement becomes a serious consideration when, in each generation, you want to give a score to hundreds of individuals so that you can identify the top end of the distribution: the few individuals with extreme scores that will become the breeders for the next generation. The silver fox study was therefore heroic, because the researchers invested the countless hours needed to assign a tameness score to each fox. In the wheel running study, measurement was automated. Garland and colleagues tested mice at 6-8 weeks of age. A mouse was placed in a standard plastic lab cage that had a hole cut in the side. A short tube inserted into the hole gave the mouse an access tunnel into the activity wheel. An activity wheel is a squat cylinder, about 36 cm in diameter, with wire mesh sides and clear plastic ends. An axle runs through the center of the ends, and the cylinder is mounted, like a car tire, so that it can spin freely.

A mouse placed into one of these cages will, during its activity period, voluntarily enter the wheel and run. When the mouse runs on the wire mesh, the wheel rotates and a photocell attached to a computer provides a way to count the number of revolutions of the wheel. Each generation, the Garland group measured the wheel running activity of about 600 mice. Each mouse spent six consecutive days in a wheel cage, and the researchers took as its final score the average number of daily wheel revolutions on days five and six. At any time during measurement, the experimental rooms had 200 wheels running.

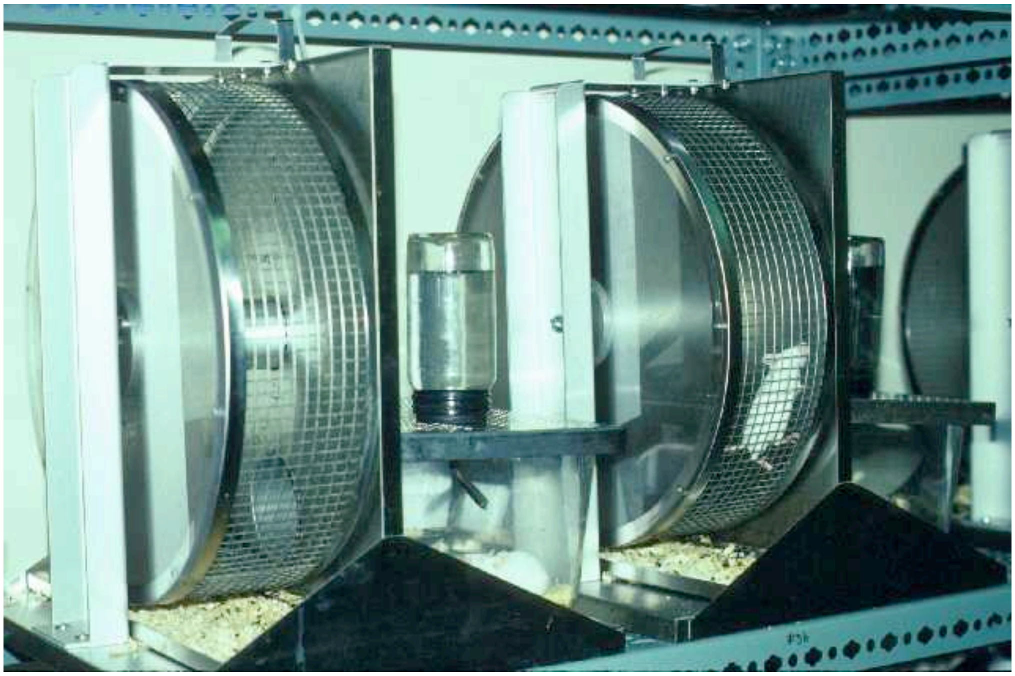

Figure 8.5. Running wheels in the Garland laboratory. Photo courtesy of Theodore Garland, Jr.

The main reason why so many mice had to be run was that the Garland group worked with replicated lines. A line is a population of mice that one maintains in the laboratory as an isolated breeding unit. Each line is a selection experiment and thus an independent replication of the experiment. The Garland group elected to create 8 lines. In each of four experimental lines, individual mice were chosen for breeding based on their wheel running scores. Only the highest-scoring individuals in each family were allowed to breed. The other four lines were controls. In each control line, individuals were selected randomly for breeding, disregarding their wheel running scores. The purpose of the control lines is to be sure that any change observed in the experimental lines is due to selection, and not due to some unknown change in laboratory conditions. Control lines also provide a reference point against which changes in the selected lines can be measured.

Results for the Garland experiment, through 60 generations, are shown in Figure 8.5. At the start of the experiment, all mice ran at about 5,000 revolutions over the 2-day test period. Control lines continued to run at about this level, but the experimental lines showed a rapid response to selection. By about generation 16, mice in the experimental lines ran more than twice the original level, and this elevated running persisted over the next 44 generations.

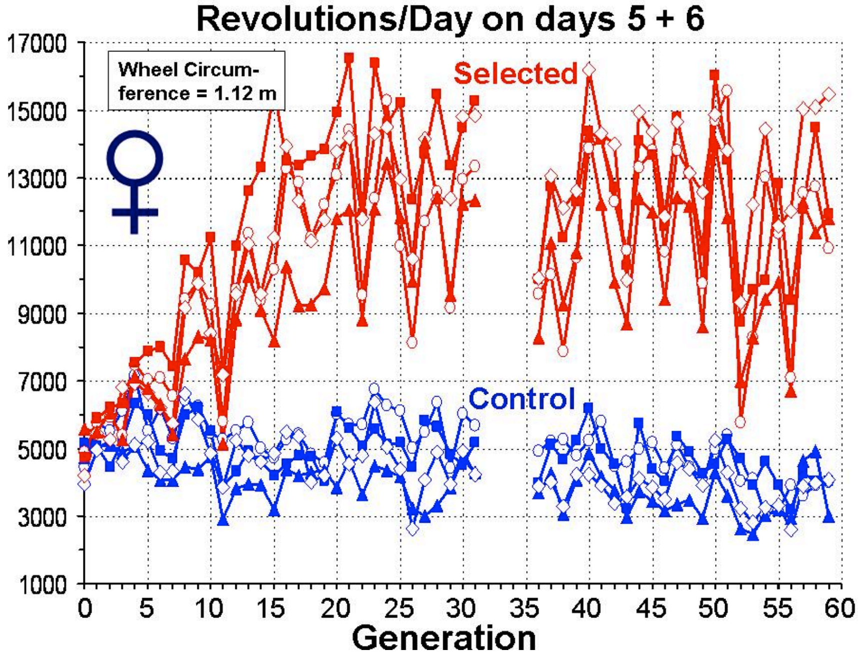

Figure 8.6. The results of the Garland wheel running selection experiment show the mean wheel running of female mice on days five and six of a six-day exposure to wheels. The experiment comprised four replicate lines of

mice that were selectively bred for high voluntary wheel-running behavior and four unselected control lines. The gap in the lines at generation 32 reflects a four generation interval when Garland and his mice moved from the University of Wisconsin-Madison to the University of California, Riverside. Figure courtesy of Theodore Garland, Jr.

The Garland experiment is unique in longevity, bit is even more so in the thoroughness with which the team explored the consequences of selection on a behavioral trait. Working with many collaborators, Garland examined how, exactly, the selected mice created more revolutions per day, how they were motivated to do so, whether other behavioral traits had been affected, and whether aspects of anatomy and physiology had changed. The selected mice created more wheel revolutions per day because, compared to mice of the control lines they ran faster, over shorter intervals, with shorter breaks between intervals. In their home cages, they tended to move more, and when their running wheels were locked, they showed behavioral and brain changes similar to those found in addictive withdrawal. Garland and colleagues concluded that their selection for elevated wheel running had created a mouse version of human Attention Deficit Hyperactivity Disorder. Although some aspects of muscle anatomy and physiology changed, most other aspects of behavior remained unchanged.

Thus, the Garland study was powerful proof of the central premise of animal behavior, which is that evolution will act on species to create individuals that act as if they are constantly asking themselves the question, “what should I be doing at this moment to maximize my lifetime fitness?" Suppose, for example, the environment of a wild mouse species changed, so that food became more widely distributed. Individuals that were more active, more likely to move, would be the most successful foragers. The Garland study shows that natural selection could cause an increase in activity without changing other importantly tuned behavioral priorities and responses.

Our current knowledge of behavioral genetics also provides another perspective on the nature-nurture debate. Is a particular behavioral predisposition built-in, or is it learned? Behavioral genetics, complimenting studies of behavioral development, shows that the answer is both. Most measured heritabilities of behavioral traits lie in the 0.30-0.50 range, meaning that about one-third to one-half of the variation among individuals is due to the additive effects of alleles. The remaining one-half to two-thirds of the variation is due to non-additive genetic effects and to environmental effects. Nature-nurture is a false, misleading, obfuscating, dichotomy. Genes direct the assembly of brains, and that assembly, before and after birth, is often modified by environmental effects. The structure of brains dictates the learning rules that a species will use, but that structure can only indirectly dictate that kinds of experiences that an animal will have. A complex series of interactions between genes and environment produce almost all animal behavior.

Chapter Nine

Living in Groups

In the Western penal system, one of the worst punishments, legal or illegal, that an inmate can receive, is solitary confinement. At first, it may seem odd that this is such a severe punishment. The inmate receives food and water, is not required to perform physical labor, and stays in a climate controlled cell. The cell may not be comfortable, but the inmate is not physically abused. Nevertheless, inmates report, after a week or two in the hole, that they feel insanity looming. After one or two months in solitary confinement, most display genuinely psychotic symptoms. Depending on the length of the confinement, the mental damage may be permanent, preventing the person, when eventually released, from ever fitting into society.

Why is this ostensibly mild punishment so severe? Because it is unnatural. Because it places a human in a situation for which the human behavioral mechanisms are not designed. Because humans, and their ape ancestors for millions of years, always live and have lived in social groups, and thus have brains that are designed to deal with the constantly changing circumstances that group living presents. When solitary confinement removes all social contact, the thwarting of those mechanisms, and the thwarting of the natural impulse to do something that results in reunification with the group, create pathology. Thus, solitary confinement, by any assessment, is cruel and it is certainly "unusual," in that it places a human in a profoundly unnatural setting. Solitary confinement is one of the worst forms of torture[71].

Why Live in a Group?

Some species, such as humans, are group living, but many are not. For example, in one of our close relatives, the orangutan, individuals are alone in the forest for most of their lives. An orangutan would be troubled by the confinement aspect of solitary confinement, but not by the solitary aspect. A survey of all the animals that have real brains (worms, mollusks, arthropods, and vertebrates) reveals that in most species, individuals do not live in groups. Group living is the exception, not the rule. It is not too difficult to understand why this should be so. Animals in groups must compete with other group members for resources such as food, nesting sites, resting sites, and mates. Animals in groups are more likely than are solitary animals to be infected by diseases or parasites carried by other group members. Thus, in most species, the best option for individuals is to live alone. Why, then, does group living exist at all? What benefit could outweigh the costs?

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[71] Gawande, A. 2009. Hellhole; The United States holds tens of thousands of inmates in long-term solitary confinement. Is this torture? *The New Yorker* 85(7), 36-45.

Hresko, T. 2006. In the cellars of the hollow men: use of solitary confinement in U.S. prisons and its implications under international laws against torture. *Pace University International Law Review* 18(1), 1-26.

Andersen, H.S, Sestoft, D., Lillebñk, T., Gabrielsen, G., Hemmingsen, R. & Kramp, P. 2000. A longitudinal study of prisoners on remand: psychiatric prevalence, incidence and psychopathology in solitary vs. non-solitary confinement. *Acta Psychiatrica Scandinavica* 102, 19-25.

The principal benefit was explicated by the famous theoretical biologist, William D. Hamilton, in a charming 1971 article titled "Geometry for the Selfish Herd"[72]. In the article, Hamilton invites us to envision 4 frogs, sitting at 0, 90, 180, and 270 degrees around a circular pond. A predator lurks in the pond and at unpredictable moments, lunges at the margin of the pond. We assume that if the predator lunges anywhere in the 90 degree quadrant that a frog occupies, then the frog will be captured. For example, if the predator lunges anywhere between 45 degrees and 135 degrees, then the frog at 90 degrees will be captured. So, at any given predator attack, each individual frog's probability of death is 1/4 (four 90 degree quadrants in 360 degrees). Now, what happens if the frog sitting at 180 degrees hops over to join the frog at 90 degrees? If we accept two assumptions: 1) that the predator will continue to lunge randomly within the full 360 degrees and 2) that if two frogs are in the attacked quadrant, only one of them will be taken, at random, then each of the two frogs now at 90 degrees has a 1/8 probability of death. To arrive at 1/8, we took the probability that the predator would lunge in that quadrant (1/4) and multiplied it by each frog's individual probability of being taken (1/2). Now, the frog sitting at 270 degrees still has a 1/4 probability of death. She looks over at the sweet deal enjoyed by each of the frogs at 90 degrees, and she hops over to join them. Now, by simply joining a group, her probability of death has dropped from 1/4 to 1/12 (1/4 x 1/3). Finally the frog sitting at 0 degrees wakes up, and hops over to join the other three. His probability of death now drops from 1/4 to 1/16. The essence of Hamilton's logic is that an individual, simply by joining a group, dilutes its own likelihood of being killed by a predator. Thus, insofar as individuals of a species have a mortality risk that is due to predation, they should form groups.

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[72] Hamilton, W.D. 1971. Geometry for the Selfish Herd. *Journal of Theoretical Biology* 31, 295-311.

Hamilton's explanation for the evolution of grouping tendency makes a simple, powerful prediction. Groups should be common among prey species, and groups should be rare in predatory species. The severity of individual risk of death due to predation should be the main driver of group formation. If all of my life is filled with the imminent threat of a predator attack, then my best survival strategy is to stand next to you. As the well known joke goes, if you and I are being chased by a bear, I don't need to be able to run faster than the bear - I only need to be able to run faster than you. The main prediction of Hamilton's selfish herd hypothesis is amply verified. Note that Hamilton used the word "herd," a word that usually denotes a group of hoofed mammals. Nearly all the hoofed mammals are pursued by several species of predators, and nearly all form herds. Often, the herds contain hundreds, to thousands, and sometimes hundreds of thousands of individuals. Each individual, by joining the huge group, vastly dilutes its own risk of death due to predation. In the open ocean, huge herds of fish are always formed by prey species. In contrast, one never sees herds of hundreds to thousands of lions, or of sharks. The vast differences in the grouping tendency of prey versus predator species is a consequence of individuals behaving selfishly, behaving as if they were constantly asking themselves the question, "what should I be doing at this moment to maximize my lifetime reproduction?" For most predators, the selfish optimum is to be solitary, to avoid sharing food with others. For most prey species, the selfish optimum is to crowd in close to others, even when this means giving up some food and being exposed to more disease. Better to be hungry and sick, with at least some chance of reproducing, than to be a corpse fed upon by a leopard, with no chance of reproducing. Herbert Prins, a biologist who studied African Buffalo for many years, provided a clear illustration of this trade-off[73].

Social Dominance

Even though Buffalo are large and powerful and pugnacious, they still can be killed by lions. Thus, they form herds. A foraging group of several hundred individuals assumes the shape of a narrow parabola, moving in the direction of the apex. Leading animals are at the apex and trailing animals are at the rear, open side of the parabola. Prins made visual assessments of the body condition of buffalo in these foraging groups. By using standard anatomical landmarks, a visual assessment provides a reasonably accurate estimate of the amount of fat that an animal carries. In nature, fat is good, and animals almost never have enough. Individual buffalo at the leading edge of the foraging groups were in the best condition, and those at the rear were in the worst condition. At the front, individuals find fresh grass. At the rear, individuals find not-so fresh grass that has been picked over and trampled by the preceding 200 buffalo. Differences in condition would thus emerge if individual position in a foraging group was consistent over time. In other words, some individual buffalo are always at the front of a foraging group, getting the first pick at a patch of grass as a group approaches it. Other individuals are always consigned to the rear, where they try to find something to eat in the trampled, dung-spattered leavings of the herd. Trailing animals are not able to move up in a foraging group because the individuals in front of them will not yield position. Each individual is trying to maximize its own

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[73] Prins, H.H.T. (1996). Behaviour and Ecology of the African Buffalo: Social inequality and decision making. Chapman & Hall, London.

lifetime reproduction and therefore it is unwilling to share. A Buffalo herd is indeed a selfish herd, as are the herds of most animal species. Some buffalo have high social status and they are able to claim a place at the front edge of a foraging herd. Others have low social status and they are not able to follow their foraging preferences because others prevent them from doing so.

The individual differences in status among Buffalo are the result of a phenomenon known as social dominance. Social dominance is the primary organizing force in animal societies, and it is nearly ubiquitous in the species that form groups. It was first described by a Norwegian biologist, Thorlief Schjelderup-Ebbe, in his 1921 Ph.D. dissertation on the behavior of domestic chickens. Schjelderup-Ebbe noted that if 10 or so hens that were strangers to each other were placed together in a pen, then a flurry of short-lived attacks and retreats would ensue. Hen A, with her head held high, quickly steps toward hen B and pecks at her. The beak may or may not make actual physical contact. Hen B turns away and steps away. Typically, what happens next is that is that Hen A now turns and pecks at hen C, or hen C, having seen hen B lose, approaches and pecks at B[74]. After a day or so, these overt attacks subside, as the hens settle into an established peck-order (Schjelderup-Ebbe's term). In an established peck order, assertions of dominance and signals of subordinate status continue, but they become more fleeting and subtle.

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[74] Chase, I. D. 1982. Behavioral sequences during dominance hierarchy formation in chickens. *Science*, 216, 439-440.

In a group of 10 or fewer hens, the peck order will be linear, meaning that there is one hen at the top, that dominates all other hens, that there is a hen second in rank that dominates all other hens except number one, and so on until we arrive at the bottom ranked hen, that dominates no other hens and is the target of all. The data from one hour of observation of wins and losses in these brief, formal-looking encounters for a group of 5 hens, would look something like this:

LOSER

	LOSER					
		A	**B**	**C**	**D**	**E**
WINNER	**A**		5	7	4	6
	B			8	6	4
	C				5	7
	D					3
	E					

Figure 9.1. A win-loss matrix, showing counts of dominance encounters
between all pairs in a 5 member group

The dominance hierarchy shown in figure 9.1 is perfectly linear, but not all dominance hierarchies are so. For example, data representing encounters of 5 individuals in a different group might look like this:

		LOSER				
		A	**B**	**C**	**D**	**E**
WINNER	**A**	▨	6	7	5	8
	B		▨	7	0	10
	C			▨	8	6
	D		8		▨	6
	E					▨

Figure 9.2 - A win-loss matrix for another group, in which the dominance hierarchy is not perfectly linear

This dominance hierarchy is not perfectly linear. It contains one set of relationships that is called a circular element. The circular element here is that B is dominant to C, and C is dominant to D, but D is dominant to B. In a win-loss matrix, circular elements are revealed by entries that appear below the principal diagonal (designated by the shaded cells). Generally, as group size increases, the number of circular elements increases. Several investigators have developed statistics to assign a linearity score (from 0, meaning perfectly nonlinear, to 1, meaning perfectly linear). These statistics take into account group size (in very small groups, linearity easily can arise by chance) and the number of circular elements[75].

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[75] See, for example, de Vries, H. 1995. An improved test of linearity in dominance hierarchies containing unknown or tied relationships. *Animal Behaviour* 50, 1375-1389.

In essentially all but the most transitory animal groups, social dominance is apparent. As is so for Buffalo, social dominance creates inequalities. Dominant individuals have priority of access to resources and subordinate individuals do not. Specialized, subtle movements that signal domination or subordination exist, and these signals pass between individuals regularly. As a result, social groups usually appear to function with apparent ease, with little overt tension to ruffle the smooth facade of harmony. However, social dominance and the signals that support it do not exist to create a group benefit. They exist because individuals are following their own selfish interests, and those interests include minimizing the time and energy wasted on disputes. Subordinate individuals accept their daily rounds of humiliation and their diminished access to resources because the alternative would be to live apart from the risk-diluting safety of the group.

What determines the dominance status that an individual acquires? We do not have a complete answer to this question, but we do know of two main effects. The first is an obvious one: size. In a social group, dominance status generally reflects relative body mass. Larger individuals become dominant. Although they may never fight with others, their larger size predicts that they would win if a fight occurred. Animals usually are quite skilled at assessing the fighting ability of a rival by observation alone, and this skill results in the acknowledgment of social rank. The dominance ranking of two individuals is essentially an agreed-upon concession of what the outcome of a fight would be. Thus, dominance rank is not always completely accurate, and an individual that challenges its rank by fighting may sometimes rise in rank. The existence of dominance hierarchies illustrates the fact that animals in nature are very reluctant to fight. Fighting is rare because in most disputes, the fitness benefit of winning does not outweigh the fitness cost, which is expressed as the risk of injury or death.

The other main effect of dominance status is prior experience. An animal that starts life with a series of winning encounters tends to become dominant. An animal that starts life with a series of losing encounters tends to become subordinate. In essence, animals are programmed to adjust their assessment of the fighting ability of a rival based upon their own personal history. This mechanism, which has been demonstrated in many species, is the primary basis for the stability of dominance hierarchies. Individuals start down one track or another, and the self-fulfilling nature of the prior experience adjustment mechanism keeps them on that track.

This effect was first shown in a laboratory experiment on inbred lines of house mice[76]. Inbred lines are produced by many successive generations of brother-sister matings. The result is a stock of mice that are all genetically identical. Thus, inbred lines are useful, because any differences that are observed among individuals must be due to environmental effects. Ginsburg & Allee gave one group of mice a series of losing encounters by pairing them time after time in a neutral arena with an older, heavier mouse or a mouse of a more aggressive strain. They gave another group a series of winning encounters by pairing them with a series of younger, lighter opponents or a mouse of a less aggressive strain. Then they paired individuals from the two groups. In each pairing, the

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[76] Ginsburg, B. & Allee, W. C. 1942. Some effects of conditioning on social dominance and subordination in inbred strains of mice. *Physiological Zoology* 15, 485-506.

two mice were identical in age, weight, and genotype; they differed only in the nature of their prior experience. Prior experience predicted perfectly which mouse would win: winners always won, and losers always lost.

The prior experience effect is not just a laboratory phenomenon. In nature, there are many sources of variation in early experience that operate to set individuals on a particular dominance trajectory. A particularly clear example is provided by pronghorn, the species that I study[77]. Pronghorn individuals are usually found in groups, and in these groups dominance interactions are common. Pronghorn display three kinds of social interaction that have nothing to do with competition for resources but are pure assertions of social dominance. In a simple displacement, the initiator stares at a target animal, then approaches with the head held high. If the recipient does not immediately turn away and walk away, the initiator butts at the recipient, causing it to move away. Feeding displacements occur when pronghorn are actively feeding, an activity that occupies about 40% of their days. Unlike Buffalo groups, a group of pronghorn forages in a rough line, with the direction of movement perpendicular to the line. The initiator of a feeding displacement stops feeding, walks directly over to another feeding individual, and lowers the head in an intention to butt. The recipient relinquishes its feeding line and steps away. The initiator may or may not start feeding where the recipient fed. A bedding displacement occurs when some animals in a group are reclined. The initiator walks toward the reclined recipient and lowers the head. The recipient stands up and walks away. Typically, the initiator reclines in that spot. Year round, these interactions occur in groups of pronghorn

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[77] Byers, J.A. 1997. American Pronghorn. Social Adaptations and the Ghosts of Predators Past. University of Chicago Press, Chicago.

at a rate of 1-2 interactions per animal per hour. Within sex, individuals are arrayed in a mostly linear hierarchy, with a small number of circular elements.

In pronghorn, the prior experience effect is predominant in the determination of dominance rank, and the effect occurs because of differences in relative birth date. Pronghorn fawns are born from mid-May to mid-June. Birth mass is about 4 kg, and the fawns grow rapidly, gaining about 0.25 kg per day. During the first three weeks of the fawn's life, the mother and fawn practice the hiding strategy. If the fawn survives those first three weeks, then the mother brings it into a summer groups of other females and fawns. As the summer groups form, fawns of differing ages meet with each other. Because of the fast growth rates, a fawn that is 4 days older than another is 1 kg heavier and noticeably larger. Fawns compete with each other for social dominance, using the three types of interaction - simple, feeding and bedding displacement - that adults use, but the interactions are much more brutal. When an adult lowers it head to displace another, there is rarely physical contact. Fawns, in contrast, violently butt each other. When the groups first form, the rate of dominance interactions among fawns is about 10 times the adult rate. In about 2 weeks, the rate settles down to twice the adult rate and it remains at that level until the fawns are weaned and the summer groups begin to break up. In the summer groups, all male fawns become dominant to all female fawns, but, within sex, a fawn's rank is set by its relative birth date and hence its relative size. Early born fawns are larger than later-born fawns, and they use their size advantage in the early dominance fights. By the end of the summer, the same-sex fawns in a group are arrayed in a linear hierarchy, that is perfectly coincident with their relative birth dates. Individuals then keep this dominance ranking for the rest of their lives. Their early experience in fawn groups has given them differing levels of self-confidence. When she is one year old, and still at about 75% of her final adult weight, a female that was born early in her year meets for the first time a much heavier 4 year-old adult that was born late in her own year. The yearling always wins.

Another kind of prior experience effect occurs in many species of monkeys and apes. Most primates (orangutans excepted) live in social groups that comprise several mother families (females and their female descendants) and several unrelated adult males. When they reach sexual maturity, males that were born into a group usually are evicted by resident males; they are forced to disperse to find a new group to join. Dominance is well developed in primates and it is often reinforced by facial expressions or slight shifts in posture. Dominance is also a characteristic of mother families. A female typically rises to a social rank that is just below that of her mother, and so one entire mother family can be dominant to another. A young female reaches her final rank because mothers intervene in dominance disputes between juveniles. A mother can only intervene on her daughter's behalf if she herself is dominant to the mother of the other juvenile. Thus, a young female becomes dominant to all female peers whose mothers are subordinate to her own mother.

In hamadryas baboons, a large ground dwelling monkey, researchers showed that individuals seem to be aware of these dominance complexities[78]. The researchers played recordings of the vocalizations characteristic of a dominance dispute to experimental subjects in nature. Previously obtained recordings of the vocalizations of many individuals

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[78] Bergman,T. J., Beehner,J. C, Cheney, D. L, & Seyfarth, R. M. 2003. Hierarchical Classification by Rank and Kinship in Baboons. *Science* 302, 1234-1236.

allowed the researchers to manufacture an apparent squabble in which a dominance reversal was occurring: an individual that had been subordinate to another was now, according to the manufactured playback sounds, becoming dominant to that individual. The researchers played sounds suggesting two types of dominance reversal. The first was a reversal within a mother family. The second was a reversal between families, which is a more profound upsetting of the social order. The researchers then recorded the number of seconds that the experimental subject spent looking in the direction of the hidden loudspeaker. A playback of sounds suggesting a within-family dominance reversal elicited about 2 seconds of looking. A playback suggesting a between family dominance reversal drew attention for twice as long: about 4 seconds.

Territory

Social dominance is selfish behavior that is designed to ensure priority of access to potentially contested resources at any future time. A similar kind of behavior, that also works to lay advance claim on resources, is called territoriality. The essence of territorial behavior is that an animal actively defends the boundaries of a defended area. Defense takes the forms of advertisement that the space is occupied (bird song, for example), patrolling to monitor territory boundaries, and aggressive eviction of intruders. Territorial behavior thus has a cost, expressed in terms of the time and energy that are devoted to defense, that ultimately can be reflected as a potential decrease in fitness. Counterbalancing the cost must be a greater fitness benefit. The benefit comes about by the exclusive use of the food, refuge, nursery sites, or breeding opportunity that the defense of the territory provides. The fitness advantage of laying advance claim on property is general and robust. On a calm early morning in the Caribbean, while I sipped coffee at the rail of a cruise ship and contemplated the water, the peace was broken by a strident mother from New Jersey, who directed her daughters in loud, nasal tones to tie towels around the tops of twelve adjacent deck chairs. Satisfied that her territory had been claimed, she marched her brood to breakfast.

Territoriality has been described in hundreds of animal species, including limpets, crickets, butterflies, flies, ants, wasps, bees, spiders, snapping shrimp, frogs, salamanders, turtles, alligators, lizards, fish, birds, and mammals. The resources claimed by territorial defense vary from mating opportunity alone to all-purpose areas where mating, feeding brood rearing, and sheltering occur. Similarly, territory sizes vary greatly, from tiny areas equal in diameter to about 4-5 of the owner's body lengths, to huge areas, equal in diameter to thousands of the owner's body length.

Bumper Cars in a Washing Machine

Limpets are snails that live on rocks at the ocean tideline. The suction that they create with a muscular foot keeps them in place on wave-pounded vertical slabs of rock. A limpet crawls slowly across the rock, using its radula, a tongue-like scraping organ, to harvest the algae that carpet the wet rocks. Limpets are territorial. Each individual defends a patch of rock and by keeping others out ensures that the algae are harvested at a rate appropriate to maintain a steady supply. Territory owners shove intruders and may dislodge them from the rock, casting them into the surf below and almost certain death.

Marsh Life

In spring across most of North America wherever there is a reedy pond or marsh, male red-winged blackbirds announce their presence. A male hunches forward, elevates his wings slightly to show off the brilliant red-orange patch of feathers on his shoulders, and emits a penetrating (some would say grating) squawk. Each male is displaying on his own territory, a small patch of water and reeds to which one or more females will be attracted. From his perch, each male can survey his entire territory and he can quickly fly to chase away an intruder that appears anywhere along the boundary. A territory contains sites where a nest can be built and it contains enough area to provide the insects that the male, his mate, and especially their broods will require. Males that defend high quality territories with good nest sites and abundant food may attract several females and thus will father several broods of chicks. Peripheral males on poorer territories near the marsh edge may attract only one female or perhaps none. In red winged blackbirds, males compete for mating opportunities by laying advance claim to the resources that females need to rear a brood of chicks. This is a very common sexual theme.

Disposable Soldiers

All species of ants live in colonies in which one or a few reproductive females lay all the eggs and most females are sterile workers that perform all the tasks (nest construction, cleaning, brood care, food gathering, nest defense) needed to maintain the colony. All ants vigorously defend the nest against intruders and, in addition, many species defend a large territory surrounding the nest. An ant colony is particularly well suited to territorial defense because thousands of workers can be in many places at once. A territorial limpet may suffer considerable damage to its algal lawn by an intruder before it discovers and deals with the challenge. In contrast, an ant colony can have many individuals on patrol at all daylight hours. These individuals can run back to the nest to recruit help if they detect an intruder, and they willingly die in fighting. From the perspective of the reproductive unit, the colony, the loss of a few hundred workers imposes a slight energy cost, which translates into little or no fitness cost[79]. Ants can run a "police state" type of territorial defense at relatively low cost and hence have some of the most absolutely defended territories known among animals.

Original Speed Dating

The African Kob is a medium sized (80-100 kg) antelope that ranges across a narrow belt of sub-Saharan Africa. Males defend territories. Each territory is a tiny circle, about 15-30 meters in diameter. Territories are packed together into clusters of about 15, so each male has several territorial neighbors. However because the territories are so tiny compared to the size of the animal, a male can easily survey his entire territory boundary and can jump

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[79] Holldobler, B. & Wilson, E.O. 1990. The Ants. Harvard University Press, Cambridge, Massachusetts.

to defend anywhere that a rival crosses the line. Kob eat grass, so such a small circle cannot support even a single animal. A male retains his territory for as long as he can, until he must leave to eat and regain all the fat that he has lost while defending his little dirt patch. Clusters of tiny territories such as these are called leks, and they exist for one purpose only: mating. Females visit leks to find a sire, and the packed collection of males permits a quick comparison of what is on offer. A female kob typically enters a lek, moves among territories, and then chooses one male as the sire of her next calf. The criteria that females use to make these comparisons are not completely understood, but one preference seems to be for males that occupy territories at the center of the lek. Leks are not unique to Kob; they are the main way that males compete for matings in about 200 species of beetles, flies, butterflies, wasps, fish, amphibians, birds, and mammals. A recent human convention that embodies the same idea is called speed dating.

Nursery Defense

The Garibaldi is a stout, brilliant orange fish that lives in rocky areas along the Pacific coast of North America. Males choose an area that they will defend and then they aggressively chase away all other fish and invertebrates. A male works diligently to pluck a patch of rock until it is completely bare. The bare surface then is colonized by one species of red alga, and the male continues to work hard to maintain a clean, pristine surface of this alga alone. The preparation and cultivation of an algal mat may require two years of steady work, and the intensity of a male's territorial defense is testimony to the magnitude of his investment. Garibaldi males are so focused on territorial defense that they only reluctantly back away even from human scuba divers. A female Garibaldi visits male territories, selects an algal mat that she likes, and deposits her eggs there for the male to fertilize. The female then leaves and the male continues to defend a territory around his nursery until the eggs hatch and the fry disperse. In this example of territoriality, not only is there defense of a resource, the resource itself is created by the animal.

Who Benefits?

Social dominance and territoriality, two of the most common expressions of social behavior, illustrate the rule of individual selfishness in animal social behavior. Behavior, like other aspects of phenotype, such as the length of the small intestine, or the shape of a molar tooth, evolves because of individual differences in reproductive success. Thus, behavioral traits, over evolutionary time, become tuned to maximize individual fitness. Recall from Chapter 3 that fitness is a measure that shows the magnitude of an individual's lifetime reproduction compared to the magnitude for the individuals with the highest lifetime reproduction. Thus, individual fitness can increase by an increase in an individual's reproduction, or by a lowering of the reproduction of others.

In a dyadic social interaction, there is an actor, that performs a motor pattern or linked series of motor patterns, and there is a recipient, the individual that receives the consequences of the action. In such a social interaction, there are four possibilities for the combined fitness effects of the action on the actor and on the recipient, shown in the table below.

ACTOR FITNESS		RECIPIENT FITNESS	
		+	-
	+	COOPERATION	SELFISHNESS
	-	ALTRUISM	SPITE

Figure 9.3 - In a dyadic social interaction, there are four possibilities for the joint fitness consequences of the act on the actor and the recipient.

The first general prediction that we can make from this table is that actions in the second row, those that reduce the fitness of the actor, should not occur. Evolution weeds out behavior such as walking up to a predator and exposing the throat, and the same logic applies to social behavior. Fitness reducing acts are always removed by natural selection. From the definition of fitness, we can make a prediction about the first row: cooperation should be rare and selfishness should be common. A dispassionate survey of how animals in nature treat each other confirms these predictions. Actions that look spiteful essentially do not occur. Actions that look altruistic are rare, but there a several well known examples. Actions that look cooperative are rare, and actions that look selfish are the norm.

Altruism

The exemplars of altruism are the eusocial insects. These are the bees, ants, and termites that live in huge colonies, in which only one or a few females lay eggs and most individuals toil as sterile workers. The workers seem to display the ultimate form of altruism; they give up all of their own reproduction in service to the reproduction by another female. In *The Origin of Species*, Charles Darwin admitted that the eusocial insects were a challenge to his theory of evolution by natural selection. How could natural selection favor individuals that gave up their own reproduction? A century later, a plausible explanation of the apparent paradox appeared[80]. The author was W.D. Hamilton, who I introduced earlier in this chapter as the author of *Geometry for the Selfish Herd*. Hamilton's primary insight was that in social groups, the degree of relatedness between two individuals is important in determining whether natural selection will promote an act that appears to be altruistic. The degree of relatedness, or *r,* that Hamilton referred to has a precise meaning in evolutionary genetics. *r* between two individuals is the probability that those two individuals, at any given site on a chromosome, will have gene copies that both came from the same ancestor. *r* between two individuals is the probability that for any gene, they share the gene identical by descent. *r* between a parent and its offspring is 1/2, between full siblings is 1/2, between half-siblings is 1/4, between a grandparent and a grandchild is 1/4, between first cousins is 1/8.

Using this definition of *r*, Hamilton defined a term that he called inclusive fitness. The concept of inclusive fitness asks us to acknowledge that offspring are simply one class of relatives, to which the parent is related by 1/2. During an individual's lifetime, besides direct production of offspring, there are other offspring, of a variety of degrees of relatedness, produced. For example, a female may produce 4 offspring in her lifetime, but during that time her sister produces 4 offspring, her aunts produce 12 offspring and her

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[80] Hamilton, W. D. 1964. The genetical evolution of social behaviour. I & II. *Journal of Theoretical Biology* 7, 1-52.

own children produce 16 offspring. Figure 9.4 shows how we calculate her inclusive fitness.

RELATIVE	N	r	INCLUSIVE FITNESS INCREMENT
OFFSPRING	4	0.5	2
NEPHEWS AND NIECES	4	0.25	1
COUSINS	12	0.125	1.5
GRANDCHILDREN	16	0.25	4

INCLUSIVE FITNESS			8.5

Figure 9.4 - An example of how to calculate inclusive fitness

Note that in this example, the female's direct production of offspring counts for only about one-quarter of her inclusive fitness. Hamilton proved mathematically that natural selection will operate on individuals to make them try to maximize inclusive fitness, not simply direct individual reproduction. Thus, when it is living in a group that contains relatives, an individual faces an allocation problem. To maximize its inclusive fitness, how should it distribute benefit (apparently altruistic acts) among those relatives?

Hamilton solved the allocation problem. First, for any dyadic interaction, we identify a Benefit (B), which is the additional fractional number of offspring that the recipient of the act will produce as a consequence of the act. Next, we identify a cost (C), which is the decrease in the fractional number of offspring that the actor will produce as a consequence of performing the act. Hamilton proved that natural selection will promote the performance of the act, as long as:

$$Br > C.$$

This inequality is known as Hamilton's Rule, and it specifies the conditions under which behavior that looks like altruism will evolve. Hamilton's prediction was that this kind of behavior will evolve when the altruistic acts are directed toward relatives. An individual animal is related to itself by $r = 1$, so Hamilton's rule for individuals in their interactions with nature reduces to the familiar $B > C$: the benefit of an act must be greater than the cost. If the individual is interacting with a relative, for example offspring where $r = 1/2$, then the benefit must be more than two times the cost. For many types of parental care, which make the difference between an offspring surviving or not, this is certainly true. Finally, at very small values of r, in a group of non-relatives, the ratio of benefit to cost must be so huge that there is no realistic circumstance that would ever promote altruism.

Several clear predictions emerge from Hamilton's Rule. First, wherever we see behavior that looks like altruism, it should be in groups of animals that contain close relatives. Second, animals should practice nepotism: when they have a choice, they should distribute altruistic benefit to relatives, and they should give benefit to relatives in amounts proportional to r. A corollary of the second prediction is that animals, especially those that live in groups that are a mix of kin and non kin, should evolve kin identification mechanisms.

Biologists started to test these predictions in the mid 1960s, about 20 years after the appearance of Hamilton's paper. Shortly thereafter, Edward Wilson of Harvard University published *Sociobiology*, the first of several books that gave him celebrity status[81]. In the book, Wilson reiterated the claims of the previous generation of ethologists, who had argued that behavior was a proper subject of biological study. However, Wilson placed emphasis on the biological study of social behavior, and he championed the approach of deriving hypotheses from evolutionary principles (as Hamilton had done) and then testing these hypotheses with observations and experiments. In the subsequent three decades, many biologists followed this approach, and we learned a lot about the social behavior of animals in nature. Before this revolution in behavioral biology, the premise that animals in nature acted as if they were constantly asking themselves the question, "what should I be doing at this moment to maximize my inclusive fitness?" was just that: a premise. Now it is solidly established fact.

Animals sometimes act in ways that seem detrimental to themselves and beneficial to non-relatives. For example, alarm calls are common. A group a columbian ground squirrels is out, foraging. A coyote appears at the edge of the colony. The first squirrel to see the coyote gives a short, high-pitched bark and runs to the mouth of its burrow. Or, it may run to the mouth of its burrow first, and then vocalize. All the other squirrels within earshot run to their burrows. Although the behavior looks like altruism, the costs are so small that they are almost impossible to measure, and the benefits to recipients are similarly difficult

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[81] Wilson, E. O. 1975. *Sociobiology. The New Synthesis.* Harvard University Press, Cambridge, Massachusetts.

to detect. Altruistic acts, that have real costs to donors and significant benefits to recipients, only occur among relatives. When we consider acts that have clear costs, such as delivering milk to non-offspring (milk is energetically rich and very expensive to produce), the pattern of kin-only benefit is obvious. In only 20 or so mammal species do mothers act to permit the delivery of their milk to young other than their own. In all of these species the mothers live in stable social groups that comprise close relatives. In species that have social groups such as herds of wildebeest or beach throngs of fur seals, mothers have evolved fail-proof discrimination mechanisms that allow them to permit only their own young to suckle.   The altruistic provision of significant benefit at significant cost always turns out to be nepotism: simply another example of selfish individuals working to maximize inclusive fitness.

This discussion brings us back to the question of the eusocial insects. Do the sterile workers conform to Hamilton's Rule? Hamilton concluded that they do, and that this is so because of haplodiploidy. Recall from Chapter Three that the Hymenoptera (bees, wasps, ants) have haplodiploid sex determination. Males are haploid (there is one copy of each chromosome per cell and thus all sperm are genetically identical). In addition, mating is decoupled from fertilization. When a female mates, she stores sperm in her spermatheca. When she lays an egg, she can decide whether to fertilize it. An unfertilized, haploid egg develops into a new haploid male. A fertilized, diploid egg develops into a female. This method of sex determination probably evolved in parasitoid ancestors of the Hymenoptera as an adaptation that allowed females to control the sex ratio of a clutch when local competition for mates was variable. Hamilton pointed out that haplodiploidy in eusocial

Hymenoptera also creates unusually high r between workers, all of whom are sisters. In the extreme case, if a queen honeybee has mated with a single male, then any pair of workers share 100% of their paternal genes identical by descent (because all the haploid sire's sperm were genetically identical), and on average they share 50% of their mother's genes identical by descent. Thus, in this example, the honeybee workers are related to each other by r = 3/4. If a worker chose to mate and to lay her own eggs, she would be related to those daughters by r = 1/2. Even when a queen mates with several males (which is typical), the degree of relatedness among workers remains greater than 1/2. Ultimately, the reproductive output of a hive is a new queen, who will be a sister of the workers. Hamilton pointed out that because of haplodiploidy, a worker can have greater inclusive fitness by laboring to see that a sister becomes a new queen than by directly reproducing herself.

Recently, several researchers, including Edward Wilson, who study the social insects, have challenged Hamilton's hypothesis, noting that it is neither necessary nor sufficient to explain the distribution of eusociality. It is not necessary, because eusociality is common in another insect group, the termites, that do not have haplodiploid sex determination, and because eusociality occurs sporadically in other animals, including a mammal, the naked mole rat. It is not sufficient, because most species of the bees and wasps are not eusocial. These researchers are correct to point out that haplodiploidy does not create an automatic path to eusociality. However, given the fact that most of the eusocial species are Hymenoptera, it is likely that Hamilton identified one of the main characteristics that predisposes an animal group to evolve toward eusociality.

Cooperation

Finally, we come to the most confusing and ambiguous cell of the fitness outcomes matrix shown in Figure 9.3. It is the upper left cell, called cooperation. Cooperation indicates social interactions in which both the actor and the recipient gain in fitness. Theoretically, interactions that represent this category are unlikely, because of the nature of fitness. Recall that fitness is defined as *relative* reproductive success, meaning that an individual can increase its fitness by increasing its own reproduction, or by decreasing the reproduction of others. Thus, interactions that at first are cooperative will tend to slide, evolutionarily, to the right, toward selfishness.

Another way to see this dynamic is through a branch of mathematics called game theory. Game theory initially was developed to model human social behavior, and especially economic behavior, but evolutionary biologists also have found it useful. This is because economic payoffs and fitness payoffs follow the same logic. Animals in nature struggle and compete in an energy economy, just as humans, in the current industrial age, struggle and compete in a money economy. In the study of cooperation, what is called two-person game theory is most commonly used. Two individuals will interact in a prescribed setting. In the simplest versions, each individual has a choice of performing behavior A or behavior B in the interaction. Thus, there are four possible joint choices of the two players, and we define a fitness payoff to one of these players for each of the four possible outcomes. For example, consider the game that has been used almost exclusively to model the evolution of cooperation: the Prisoner's Dilemma.

Two guys have robbed a bank and have stashed the money. They are arrested and are questioned separately. If both under interrogation stick to the agreed-upon story, then the authorities will have to release them and they will share the money. However, if one agrees to testify against the other, the authorities will release him and he will keep all the money. So, each person has the choice to cooperate (stick to the story) or to cheat (rat out the companion and take all the money, sending the companion to prison). We write the payoffs for player 1 as follows:

		Player 2	
		Cooperate	**Cheat**
Player 1	**Cooperate**	R = 3	S = 0
	Cheat	T = 5	P = 1

Figure 9.5. Payoffs to player 1 in the Prisoner's Dilemma game.

R is the Reward for Cooperating, S is the Sucker's Payoff, T is the Temptation to Cheat, and P is the Punishment for Mutual Cheating. Mathematically, the Prisoner's Dilemma game is defined as:

$$T > R > P > S$$

and

$$R > (T + S)/2.$$

The payoff matrix has what is called a saddle point, a cell in which the value is minimal in its row and maximal in its column. Not all payoff matrices have a saddle point, but this one does. If the game is played repeatedly, the saddle point represents the strategy that all individuals will ultimately adopt. In biology, it is referred to as an Evolutionarily Stable Strategy, or ESS. Here, the saddle point is the lower right-hand cell: mutual cheating.

Whether the Prisoner's Dilemma game is completely accurate in its representation of the interactions that animals have in nature is not that important. The Prisoner's Dilemma game simply provides a good general picture of the forces that conspire against the stability of cooperation between non-relatives in nature. There is always the temptation to cheat. For this reason, nearly all the interactions in nature that look like cooperation turn out to be between relatives, where inclusive fitness considerations remove the reward for cheating.

Alpha and Beta Manakins

A good example of what most behavior that seems to be cooperation between non-relatives looks like occurs in lance-tailed manakins. The manakins are a Family (Pipridae) of neotropical fruit eating birds. Most species have a lek-based mating system. On their small territories, males try to attract mates by acrobatic displays that involve short flights, hops, and very unusual movements to the wings to produce buzzing or snapping sounds.

Lance-tailed manakins have mate attraction displays of this sort, but they add an element. Unrelated males often display as pairs, performing coordinated song and dance[82]. For example, in the leapfrog dance, (image C, Figure 9.6) two males stand in line on a cleared section of a branch called a display perch. A female stands, facing them. The male closest to the female leaps vertically, gives a call, and hovers briefly before landing just behind his takeoff point. While he hovers, the male behind him shuttles forward underneath to take up the forward position. He then leaps upward and the males continue leapfrogging and calling for 10-45 seconds (see Figure 9.6 c). Although the two males seem to work equally hard in display, they do not share equally in rewards. The two males are designated as Alpha and Beta because one of them (the Alpha) fathers all the chicks produced by copulations in the display area of the two males[83]. Emily DuVal, who discovered that alpha males have exclusive mating rights, also tracked the fates of several Beta males. She found that Beta males sometimes, but not always, ascended into Alpha status when the Alpha disappeared. So the coordinated courtship looks like cooperation. The Beta male helps out his partner and in return gets a chance to become an Alpha. Also, it may be that all the practice in display helps him to become more proficient.

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[82] DuVal, E. H. 2007. Cooperative display and lekking behavior of the lance-tailed manakin (*Chiroxiphia lanceolata*). The Auk 124, 1168-1185.

[83] DuVal, E.H. 2007. Adaptive advantages of cooperative courtship for subordinate male lance-tailed manakins. The American Naturalist 169, 423-432.

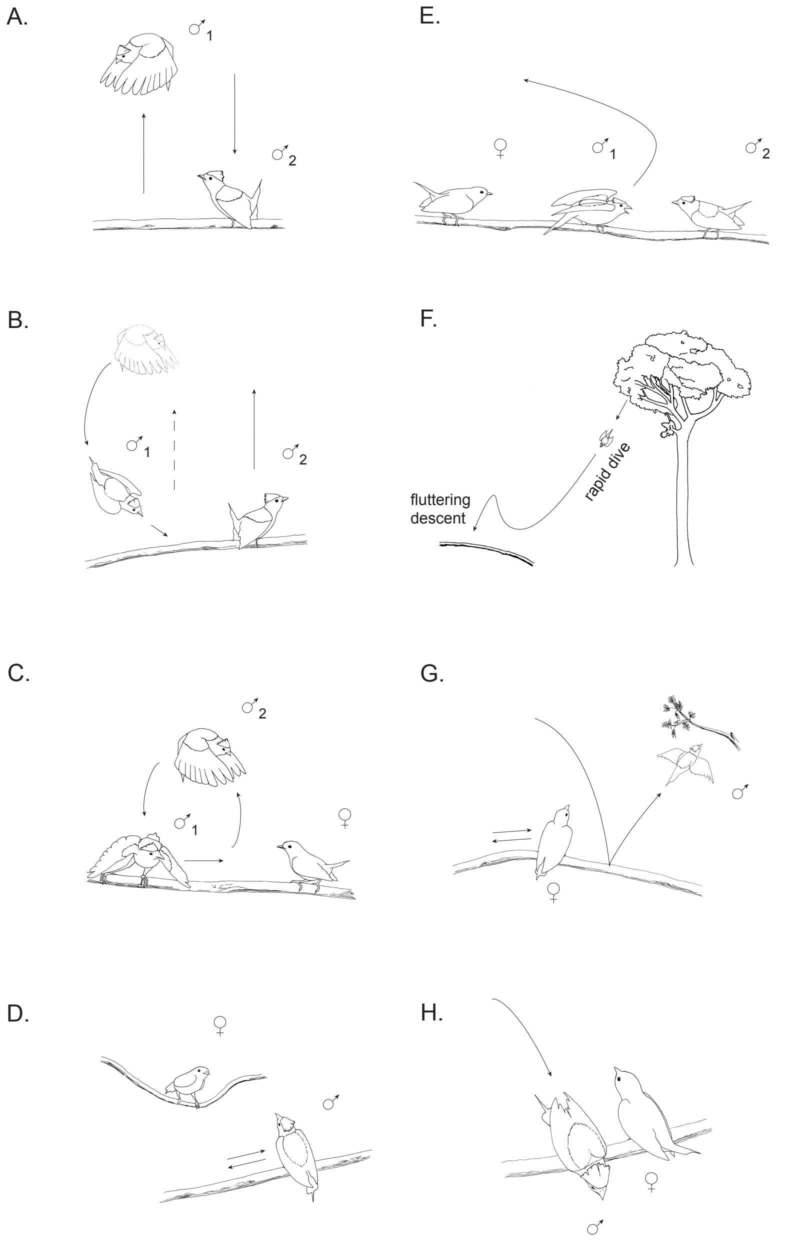

Figure 9.6. Solo and cooperative displays of male lance-tailed manakins, as represented in: DuVal, E. H. 2007. Cooperative display and lekking behavior of the lance-tailed manakin (*Chiroxiphoa lanceolata*). *The Auk* 124, 1168-1185. Original artwork by Julian Kapoor.

However, there are still several missing pieces of evidence. First, not all Beta male ascend when their Alpha disappears. Second, some Alphas have no Beta and they appear to have no difficulty in attracting females. Third, DuVal does not know at present whether pairs of males are better at attracting a female or at persuading her to mate. However, these are questions that DuVal is currently investigating. At present, it is not clear whether the Alpha male receives any benefit from having a Beta male.   Considerations of this sort make the study of cooperation challenging and confusing.

Penguin Huddling

True cooperation, however, appears to occur in Emperor Penguins, large birds native to Antarctica that have a bizarre incubation routine. Pair formation, mating, incubation, and chick rearing occur in terrestrial Antarctica. After a pair of birds mates in the Antarctic fall, the female lays a single egg. The male positions this egg on top of his feet and covers it with a fold of skin and feathers. To survive, the egg must be kept off the ice and must remain hot. The female then leaves, to feed for about 110 days in the nutrient rich waters off the Antarctic coast. The male incubates the egg, balancing it on this feet throughout the Antarctic winter. Because the male has no chance to feed during this time, and because he must endure very cold temperatures and howling winds, his ability to keep the egg alive throughout its development depends on a careful metering of the rate at which he burns his stored fat. If he runs out of fat before the end of incubation, he will not be able to maintain the proper temperature. The egg will die and he may as well.

Males meet this energetic challenge by cooperative huddling. During about 30% of each day, and especially when wind speed increases, the males group together in to very tightly packed huddles of hundreds to thousands of individuals. Because the males are crammed together more tightly than Japanese subway passengers at rush hour (about 21 penguins per square meter), individuals in the interior of the huddle experience ambient temperatures that are much warmer than the outside air temperature. When the prevailing air temperature is -40 C, the temperature surrounding a bird near the center of the huddle is balmy, close to + 37C.

Figure 9.7. Emperor penguin males huddling during an Antarctic blizzard. Reproduced from: Gilbert, C., Blanc, S., Le Maho, Y. & Ancel, A. 2008. Energy saving processes in huddling emperor penguins: from experiments to theory. *Journal of Experimental Biology* 211, 1-8

Individuals join huddles from the rear and eventually exit from the front. A joining individuals does not try to force his way into the interior. He simply plasters himself against the rear most rank and waits until group movements and penguins joining behind him carry him into the interior. The movements within these huge, tightly packed groups are accomplished by coordinated stepping. At 30 to 60 second intervals, each male takes a tiny, 5-10 cm step forward. This stepping sweeps through the group in a fast traveling wave[84]. Thus, the group can remain tightly packed (moreover, the movements act to promote the tightest possible packing, similar to the action of tapping on a jar of flour to increase density), but can still move.

By joining a group and participating in the coordinated stepping, a male can lower his metabolic rate by 20% to 30% and thus burn about one-half of the fat that he would if he stood alone. Thus, he can survive the 110 day fast, and keep the egg balancing on his feet warm and alive. By cooperating in this way, the males create a fitness advantage that would not exist if they did not cooperate. Importantly, all male share equally in the benefit, and there is really no way to cheat.

Most apparent examples of cooperation turn out to be selfishness in disguise, or, like the coordinated dances of Alpha and Beta Lance-tailed manakins, ambiguous. However, Emperor penguins show that true cooperation can arise, when the conditions are just right.

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[84] Zitterbart, D.P., Weinecke, B., Butler, J.P. & Fabry, B. 2011. Coordinated movements prevent jamming in an Emperor penguin huddle. PLoS ONE 6(6): e20260. doi:10.1371/journal.pone.0020260

Chapter Ten

Communication

In most animal species, whether or not individuals live in social groups, behavior that is specialized to alter the behavior of others is present. The word “specialized” has a distinct meaning in Biology. It means that the trait in question is derived from some other trait and that it shows clear evidence of modification by natural selection to accomplish a specific new task. For example, the outer two ear bones of mammals, the malleus and incus, are specialized. They are derived from the bones that formed the jaw joint in the reptile ancestors of mammals. The bones became greatly reduced in size and acquired a new role in sound reception as the early mammals acquired a new, stronger jaw joint that excluded these bones. Similarly, most communicative acts, behavior that animals perform with the goal of altering the behavior of others, are derived from other kinds of behavior, including respiratory movements, urination and defecation, thermoregulatory movements, protective movements, and intention movements. In an intention movement, an animal begins to perform an action and then stops. For example, if you walk toward a robin that is feeding on a lawn, at some distance the bird will stop feeding to watch you. If you walk closer, then the bird will crouch and elevate the wings slightly. This is a flight intention movement. If you walk still closer, then the intention movement will turn into an upward jump and flight. If you back away, then the robin will rise out of its crouch and will re-tuck the wings. An intention movement is a way that an animal prepares to perform an act, but it does not commit the animal to perform the act. That the postures and actions used in communication are derived and modified from other types of behavior, such as protective reflexes or intention movements, is another of the amazing insights of the Nobel laureate Niko Tinbergen[85].

Tinbergen's hypothesis, which concerns province number four - evolutionary history - of his four questions, went as follows. Imagine that an individual is in a social situation in which its fitness could be enhanced by altering what another animal was likely to do. Perhaps it is in a standoff with a territorial neighbor. If the animal performs an intention movement to strike the other and this causes the other to back away, then natural selection will favor individuals that are increasingly likely to perform the intention movement in that circumstance. Further, natural selection will favor the modification, perhaps exaggeration, of the movement, if this modification results in a more certain response from the recipient. Tinbergen referred to the evolutionary process in which an initial act becomes modified to have more reliable signal value as ritualization. Tinbergen further proposed that eventually, the new signal would no longer require the original brain activity that created the intention movement; it would acquire new control. Tinbergen referred to this change as emancipation.

By this point in the book, it should not be too surprising to you that communication is about an individual animal selfishly trying to change what another animal does. In some instances, the sender of the communicative signal and the receiver of the signal have at least a partial common goal. In other instances, the sender and receiver are in direct conflict. As an illustration of these principles, as well as of methods that researchers use in

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[85] Tinbergen, N. 1952. "Derived activities: their causation, biological significance, origin, and emancipation during evolution. *Quarterly Review of Biology* 27, 1-32.

the study of animal communication, consider a recent study of signaling by nestlings to parents in reed warblers, and the exploitation of this signaling system by a nest parasite, the common cuckoo[86].

The reed warbler is small drab insect-eating bird that nests, as the name implies, in reed beds in Europe and western Asia. The parents construct a basket nest that is attached to vertical reed stems above water, and lay about 4 eggs. As is so for most perching birds, after the eggs hatch, both parents work hard all day long to bring food to the waiting mouths of the nestlings.

The nestlings signal their hunger by throwing the beak wide open to display the bright yellow skin inside the mouth (the begging gape) and by giving the cheeping begging call. To study this communication system, the researchers first tested the hypothesis that the begging signals of nestlings were an accurate reflection of their need for food. Researchers removed nestlings temporarily from nests, fed them in the laboratory, and then recorded the begging gape area and the call rate of the four nestlings at different intervals after feeding. They found, as the time elapsed since feeding to satiety increased, that both the gape area and the call rate increased. The nestlings signal increasing need for food by increasing their tendency to display the begging gape and by calling at faster rates. Having shown that this composite signal was a fairly accurate, honest indicator of offspring need, the researchers then turned to the responses of the parents, the recipients of these signals. In nature, the researchers studied nests that contained 2, 3, or 4 nestlings, and they

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[86] Kilner, R. M., Noble, D. G. & Davies, N. B. 1999. Signals of need in parent-offspring communication and their exploitation by the common cuckoo. *Nature* 397, 667-672.

attached a small loudspeaker to the side of each nest. When parents visited the nest, they found either their normal brood, or the brood plus the broadcast vocalizations of one additional chick, or the brood plus the broadcast vocalization of four additional chicks. The researchers then watched the nests to measure the rate at which parents brought food. They found that the feeding effort of parents (the amount of food that they brought to the nest) was largely explained by begging gape area (more chicks in the nest, more of them with mouths open) and by the begging call rate (the total number of calls per second). Just as the chicks produce a composite signal of need, so parents appear to integrate both signals to adjust their feeding effort. Because the parents and the young are in partial agreement over goals, this signaling system is essentially honest. However, parents are related to the chick by r = 1/2 and the chick is related to itself by r = 1. Thus there is the potential for a conflict of interest. The optimal feeding rate from the chick's point of view could be greater than the optimal rate from the parent's fitness perspective[87]. However, at the relatively young chick ages represented in this study, the magnitude of potential conflict was likely very small; the chick signals, the parental responses, and the outcome - continued chick survival and growth - represent the best outcome for all.

This honest signaling system is exploited by the common cuckoo, and obligate brood parasite that commonly parasitizes reed warbler nests. Obligate means that the only way for a cuckoo to reproduce is to lay an egg in the nest of another species, tricking the host parents into caring for the chick. A cuckoo female surreptitiously watches a reed warbler nest, waiting until some eggs are present and the parents are temporarily absent. The

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[87] Trivers, R. 1974. Parent-offspring conflict. *American Zoologist* 14, 249-264.

cuckoo female then flies to the nest, removes and egg, lays her own egg, and flies away. The entire duration of this stealth visit is about 10 seconds. As I described in Chapter Three, the cuckoo egg tends to hatch first, and the cuckoo chick, immediately after hatching, shoves all other eggs and nestlings out of the nest. The reed warbler parents are not obviously affected by the presence of an alien species in the nest:

> "Apparently oblivious to the destruction of their own reproductive success, the pair of warblers then feeds the imposter, even as it grows to eight times their own body weight. By 2 weeks of age, the cuckoo overflows the tiny nest, and the warblers seem to risk being devoured themselves as they perch on the cuckoo's back in order to bow deep into the enormous gape with food." (Kilner et al. 1999).

The growth rate of the cuckoo chick, in grams per day, is a little less than that of four reed warbler chicks, so the reed warbler parents are capable of delivering enough food to meet the demands of the parasite. To keep the food coming, the cuckoo chick needs to deliver signals that are equivalent to those produced by four reed warbler chicks. At first, the gape area of the cuckoo chick is only a little less than that of four reed warbler chicks, and the cuckoo chick produces begging calls at about the rate that would be produced by four reed warbler chicks. After a few days, the gape area of the single cuckoo chick becomes progressively smaller than that of four reed warbler chicks. The cuckoo chick compensates for this by elevating the begging call rate to a greedy, insistent rate of 10 to 20 calls per second. This constant yammering by the parasite chick is sufficient, along with its gape area, to induce parental feeding at the level appropriate for four reed warbler chicks.

Femmes Fatales

Cuckoos are not alone in their ability to tap into and exploit the communication system of another species. There are quite a few other examples, including the well known case of firefly femmes fatales. A firefly is not a fly, but a beetle in the family Lampyridae, that contains about 2,000 species. These beetles have, like a few other organisms, evolved the ability to produce light, and they use the light in sexual signaling. A male flies in a lengthy search pattern early in the evening, emitting a species-specific pattern of flashes. A species-specific signal is possible because the duration of each flash and the intervals between flashes can vary. Thus, each species has its own Morse code-like flash pattern. At any location, several species may be displaying simultaneously. A female moves much less. She waits until she sees the flash pattern of a male of her own species, presented in a way that indicates acceptable male quality, and then she gives a characteristic flash response. The male that sees a conspecific female response approaches and lands. The next stage of courtship begins. The flash signaling system is used to make a long range identification of the correct species and to discriminate among possible conspecific suitors[88].

Many Lampyrid beetles are predators. In several species of the genus *Photuris*, predatory females use aggressive flash mimicry to obtain a meal[89]. The watch for the flash patterns of males in one of several species of a different genus, *Photinus*, then emit the correct response for that species. When the *Photinus* male alights close to her, the *Photuris* female

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[88] Lewis, S. M. & Cratsley, C. K. 2008. Flash signal evolution, mate choice, and predation in fireflies. *Annual Review of Entomology* 53, 293-321.

[89] Lloyd, J. E. 1965. Aggressive mimicry in Photuris: firefly femmes fatales. *Science* 149, 653-654.

attacks, kills, and eats him. *Photuris* females can recognize and to respond appropriately to the signals of several different species of *Photinus* males[90].

Aggressive and Defensive Signaling

Many signals between members of a species occur, not in a mostly cooperative circumstance, as in the communication between parents and offspring, or between potential mating partners, but in a competitive context, in which the interacting individuals are in conflict. Conflict occurs because essential resources, those needed for survival and reproduction, are usually limited. The essential resources are food, nesting or refuge sites, and mates. As I wrote in the previous chapter, animals often attempt to lay advance claim to resources by social dominance or by defense of a territory. Thus, some of the most common types of signals are those that are involved in the assertion of dominant status, the signaling of subordinate status, and the advertisement of territory ownership.

Signals that assert dominance tend to be derived from attack intention movements. The dominant individual assumes an upright posture, facing directly toward the subordinate, and makes a gesture that is an intention movement to strike or is a more subtle derived version of such an intention movement. Thus in monkeys and apes (including humans), we can read dominance status by posture alone. Signals of subordinate status are derived from protective movements: the subordinate animal crouches, or hunches, or lowers the head, and turns away.

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[90] Lloyd, J. E. 1975. Aggressive mimicry in Photuris fireflies: signal repertoires by femmes fatales. *Science* 187, 452-453.

This kind of signaling, where animals are contesting dominance status or, more directly, ownership of a resource, tends to have elements that one could call dishonest. The false signaling of body size is very common. In aggressive displays, individuals adopt postures to make themselves appear larger, and they often have added physical structures to enhance the illusion. For example the Nyala, a medium-sized African antelope, uses a lateral display in male-male competition. The male turns to display its side to a rival and the apparent area of the side is increased by 40% due to fringes of hair on the spine, belly and hind legs. Similarly, male bison increase their apparent size during the mating season with a huge crown of hair on top of the head, and large dangling beard, and pantaloons, big tufts of hair on the lower legs. One of the male threat postures is to face directly toward the opponent, with the head slightly lowered. In front view, these three hair accessories greatly increase the male's apparent size. After the mating season, the males loose most of the extra hair.

More rarely, animals succeed in transmitting false information about their abilities, as well as their size. One well established example occurs in an animal species that has very dangerous weapons. The species is *Gonodactylus bredini*, a member of a group of crustaceans called snapping shrimp. These animals are predators. Their second thoracic appendage is specialized to act like a spear (the "stabber" species) or like a club (the "smasher" species) that can be extended at high speed with great force (top speeds of 24 meters per second and impact forces greater than 1,000 N)[91]. The animals achieve these blindingly fast limb extension speeds by first cocking the limb across a joint that has two internal catches, then releasing the catches to let the limb segment fly forward, similarly to the way that a crossbow is first cocked, then fired.

These lethal weapons create two constraints for the snapping shrimp. First, it is very dangerous to advance toward another animal that is in a threat posture (called the meral spread). Second, after an individual molts, there is a three day period during which the new cuticle is hardening and strikes are not possible. Finally, these animals, that live on reefs in shallow water, depend on rare cavities that they use as refuges. Individuals vigorously defend their own refuges. These conditions set the stage for dishonest signaling about ability. A newly molted individual in its refuge may be challenged by another that will take the refuge if it can. In these circumstances, the impotent resident frequently gives a meral spread threat display. The animals is giving a threat signal that it cannot back up. It is bluffing. In many instances, especially when the resident is larger than the intruder, the bluff works, and the intruder retreats[92].

Signals that advertise territory ownership are common because the alternative is continuous territory patrolling and boundary defense. If an animal can simply give a signal that an area is occupied, it may be able to devote more time and energy to other important

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[91] Patek, S. N., Nowroozi, B. N, Baio, J. E., Caldwell, R. L. & Summers, A. P. 2007. Linkage mechanics and power amplification of the mantis shrimp's strike. *The Journal of Experimental Biology* 210, 3677-3688.

[92] Adams, E. S. & Caldwell, R. L. 1990. Deceptive communication in asymmetric fights of the stomatopod crustacean *Gonodactylus bredini*. *Animal Behaviour* 39, 706-716.

tasks. Vocal signals of territory ownership therefore are common, because a vocal signal is broadcast. The sound waves emanate in a sphere around the signaler, and they pass through opaque barriers such as vegetation and they extend over the local horizon. The most well known example of vocal signaling that proclaims territory ownership is bird song. Bird song is loud and it is repetitive, two characteristics that are needed for effective advertisement. That warbler singing sweetly in a thicket is in effect screaming, "TAKEN! TAKEN! TAKEN!".

Although it is less common, vocal advertisement of territory occupancy also occurs in mammals. Wolf howling (in Yellowstone National Park, where wolves are closely monitored, the average territory size is 330 square kilometers) and lion roaring are familiar examples, but there are other less famous but equally thrilling ones. The tropical forests of southeast Asia were the evolutionary home to a group of apes called Gibbons. These primates are forest tree specialists. The Family name, Hylobatidae, means "dwellers in the trees." Individuals rarely visit the ground. They use their long powerful arms to swing from branch to branch or to sail through the air from one branch across a gap of several meters to another branch. This beautiful, unique method of locomotion is called brachiation. In the once vast unbroken tropical forests of southeast Asia, gibbons enjoyed a modest evolutionary radiation, to produce four Genera and about a dozen species. Gibbon diet is varied, but the most important component of their diet is fruit. A fruit tree is a defendable resource; it contains abundant energy that is concentrated in a relatively small space. Gibbon social groups are a mated pair and their recent offspring. Groups, and especially the mated pair, defend a territory that contains a sufficient amount of resources, especially fruit trees, to provide adequate food. Because gibbons can move rapidly through the forest canopy using their spectacular swings and flying arcs, they can physically patrol a territory and defend its boundaries. All species also announce territory ownership with loud, beautiful songs. The principal singers are the females. Their song is a series of pure, rising tones that are spaced at about one-half second intervals at the start of a song and become packed together somewhat like a bird song trill toward the end. In addition, most species sing duets, in which the male contributes either a coda to the female song or a more complex counterpoint[93]. The gibbons broadcast these loud haunting songs from the treetops, announcing their presence well beyond the boundaries of their territories.

Scent Marking

Although some mammals advertise occupancy of a territory by vocalization, the more common method is by scent marking. Nearly all mammals possess scent glands, patches of skin that are specialized to produce odor compounds. Scent glands are either modified sweat glands or are modified sebaceous glands - the oil producing glands at the base of hair shafts. Mammals also display specific scent marking motor patterns, that are designed to deposit material from the scent gland on an object in the environment. Chromatography shows that scent gland material contains dozens to hundreds of specific chemical compounds. Thus, individual or group identity can be coded by variation in the proportions of these compounds. Also, mammals commonly scent mark using urine and feces, other sources of socially significant odor. By scent marking within a territory or

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[93] Geissmann, T. 2002. Duet-splitting and the evolution of gibbon songs. *Biological Reviews* 77, 57-76.

home range, a mammal can create a zone where the odor is familiar and thus even on a dark night (most mammals are nocturnal) have a sense of whether it is home or not. In addition, although scent marks never act like an absolute “odor fence,” they do tend to slow an intruder down and to make it more nervous.

Scent marking is also used in some species to coordinate reproduction. This effect is well known, for example, in the house mouse, a superb mammal colonist. House mice have followed humans all over the globe. They are found in almost all terrestrial environments, and they even occur on remote oceanic islands that humans rarely visit. Their dispersal and colonizing ability is supported by an odor signaling system that coordinates reproduction. A male house mouse has a long, thin prepuce, that he drags across the ground to deposit a thin streak of urine. Socially dominant males scent mark like this several thousand times per night, saturating their territories with their own scent. Female mice need to smell an odor in male urine to start reproductive cycling. This compound in male urine is extremely potent. In the laboratory, exposure to tiny, microliter amounts of male urine will start mature females cycling and will accelerate the onset of reproductive maturity in young females. Male urine marking, in turn, tends to increase in the presence of odors from female urine. This reciprocal signaling system is part of the house mouse suite of adaptations that helps individuals to be effective colonists[94]. A female that has left her natal area to disperse to a new habitat does not waste energy in unproductive estrus cycles. She waits until there is a reliable indicator that males are present. A dispersing

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[94] Bronson, F. H. 1979. The reproductive ecology of the house mouse. *The Quarterly Review of Biology* 54, 265-299.

male, detecting the odor compounds indicative of female urine, elevates his rate of scent marking to provide a signal that will produce reproductively active females.

The production, detection and analysis of scents are central in the lives of most mammals. Besides scent marking to anoint personal space and to coordinate reproductive timing, mammals use odors to identify individuals, to detect levels of genetic similarity to others, to evaluate potential mates, to maintain group cohesion, to signal the presence of a predator, to attract mates, and to evaluate reproductive readiness of potential mates. Most mammals have levels of chemical sensitivity that are far greater than ours. Part of their reality is an odor world that we are only dimly aware of. To study odor communication in animals, we humans require an organic chemistry laboratory, a gas chromatograph, and other complicated equipment, just to describe the nature of the signals and to begin to alter them in the way that early ethologists studied visual signals with paper cutouts.

The other animal group in which chemical communication is nearly ubiquitous is the insects. In contrast to mammals, with scent glands that produce a complex mixture of smelly compounds that produce general responses in recipients, insects often produce pheromones, single chemical compounds or simple mixtures of compounds, that elicit specific behavioral responses from recipients. For example, in many species of ants, individual foragers lay down odor trails that lead from the nest to a food source that they have found. New foragers, exiting the nest, find the odor trail and follow it to the food source. If the recruited worker finds food there, it also lays down a scent trail as it carries the food back to the nest. In this way, a number of workers that is sufficient to quickly dismantle the food source (perhaps a dead grasshopper) and transport it back to the nest is recruited. The trail pheromones are quite volatile; they evaporate after a few minutes. Thus, old, useless odor trails do not persist. In the fire ant, a South American species that has become an invasive pest in North America, the principal trail pheromone has been identified. If one coats the tip of a glass rod with a drop of this compound (a drop is a fantastically huge amount of this substance to the ants) and holds the rod over the colony entrance, one can draw out the entire colony, as individuals climb on top of each other to try to reach the maddeningly enticing droplet.

Besides trail marking, ants use chemical communication to coordinate most activities within the colony. In their magnificent summary of the biology of ants, Bert Hölldobler and Edward Wilson[95] state that, “ The typical ant worker is a walking battery of exocrine glands...”. An exocrine gland produces compounds that are released into the environment. The responses to specific gland products are so rigid and predictable that several slave-making species of ants have evolved chemical tactics. They produce the pheromones of another species and release them when on slave raids, rendering host defense ineffective in one way or another. In one at least two cases, the aggressive pheromone release causes the members of the raided colony to attack each other while the slave makers go about collecting eggs or larvae that will become new slaves.

Chemical communication is common in the non-social insects also. In many moth species, females that are ready to mate release an attractant pheromone. Males detect the

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[95] Hölldobler, B. & Wilson, E. O. 1990. The Ants. Harvard University Press, Cambridge, Massachusetts

pheromone using their sensitive antennae. Sensitivity is so extreme that in some species, one molecule of the pheromone is sufficient to induce a neural response from the antennal receptors. A males flies toward the source of the odor until he locates the female. Courtship begins. Often, male courtship involves further chemical communication, in which the male everts brush-like scent organs near the tip of his abdomen and sweeps them back and forth across the female's head.

The sex attractant response of moth males also renders them vulnerable to human pest control measures that exploit the communication system. Agricultural research workers identify the chemical compound that is the pheromone of a pest species, synthesize large amounts of the compound, and place generous amounts inside box traps. The traps quickly become stuffed with males.

Responses to Predators

In prey species, individuals often produce communicative signals, using postures, movements, vocalizations, and scents when they detect a predator. After giving the signal once or several times, individuals may approach the predator, while continuing to signal. Typically, several other prey individuals join in the approach. The initial signaling is sometimes involved in recruiting participants. This group approach toward a predator is called mobbing. In birds, agile prey species may dive at the predator and occasionally strike it.

A common North American bird, the black-capped chickadee, lives in stable social flocks after the breeding season throughout winter. Within these flocks, individuals give two kinds of vocalizations in response to a predator. A predatory bird flying overhead elicits the "seet" call. A perched predator elicits the well known chick-a-dee call, which encodes, among other things, information about danger. This has been shown in different ways, in several studies. For example, Chris Templeton presented flocks of chickadees in an outdoor aviary with living predators that were perched in an adjacent cage. The predators ranged in size from large birds with slow maneuvering ability such as great grey owls, to small agile predators such as kestrels or pygmy owls. The small predators represent a

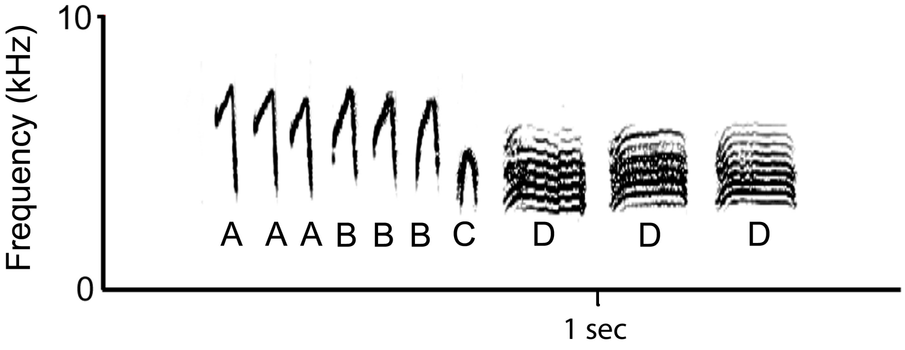

Figure 10. 1. A sonogram of the chick-a-dee vocalization. The notes labeled A, B, and C constitute the "chick" part of the call, and the notes labeled D show the nasal "dee" sounds. Image courtesy of Mike Baker.

much greater risk for the chickadees. Templeton recorded the vocal responses of the chickadees and found that the smaller, more dangerous predators elicited more calls, more D notes per call, and a shorter interval between the chick and the D portions of the call[96]. These differences suggested that the chickadees were encoding information about the relative risk of a predator in their calls. To test this hypothesis Templeton hid a loudspeaker in the aviary and played back recordings of vocalizations that had been given to a large predator and to a small predator. In response to the signal indicating a smaller, more dangerous predator, the birds gave more chick-a-dee calls and they were more likely to approach the hidden speaker. Thus, the chick-a-dee call encodes information about the relative risk of a predator and it recruits others to join in the mobbing response.

Exactly how the information on relative risk is encoded remains unclear. Other researchers, using different experimental setups, found differences in the rate of chick-a-dee calls and in the structure of the calls that were related to differences in apparent danger, but did not find, as Templeton did, more D notes in the more dangerous situation. For example, in one study, researchers presented a taxidermic mount of a prairie falcon, a dangerous predator, to single chickadees[97]. The chickadee was moved to a small cage in a sound attenuated room. When it seemed to relax, hopping around the cage and eating seeds, the researchers pulled a string that slid a cardboard barrier away, revealing the falcon mount. Thus, the chickadee suddenly saw a predator that had not been there previously. To study responses to relative danger, the researchers presented the falcon at

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[96] Templeton, C. N., Greene, E. & Davis, K. 2005. Allometry of alarm calls: black-caped chickadees encode information about predator size. *Science* 308, 1934-1937.

[97] Baker, M. C. & Becker, A. M. 2002. Mobbing calls of black-capped chickadees: effects of urgency on call production. *The Wilson Bulletin* 114, 510-516.

two distances: close (one meter away) or far (six meters away), and recorded the vocal response of the chickadee. In this experiment, the chickadees responded more quickly to the falcon mount when it was close, and gave more chick-a-dee calls. In contrast to the Templeton study, the number of D notes per call did not differ between close and far trials. The researchers also found more A notes and fewer B notes per call in the far compared to the close trials. So, like the Templeton study, the researchers found that the chick-a-dee call seems to encode information about danger, either in its repetition rate or in the proportions of notes that make up calls, but there was disagreement on the meaning of call structure, the proportions of A, B, C and D notes used. One way to resolve these differences of interpretation would be to record calls from all individual chickadees in a flock in nature that was interacting with a predator and to simultaneously record the reactions of all other birds and of the predator. Currently, the technology to do this does not exist.

Mobbing is an example of communication between, as well as within, species. The goal of the behavior is to cause the predator to go away, so that the prey individual can resume its normal activities. A particularly clear illustration of the fact that mobbing signals have evolved to influence the behavior of predators occurs in California ground squirrels. These burrowing rodents have had a long coevolutionary history with rattlesnakes, and they have evolved a number of defenses. Adult squirrels are resistant to rattlesnake venom and they can jump rapidly to avoid snake strikes. However, their pups are slower and do not yet have the chemical resistance. They need protection when a rattlesnake appears. An adult parent approaches a hunting snake and stands with its tail held upright, with the hair erected. The squirrel waves its tail from side to side (this is called tail flagging) and may kick dirt in the snake's face. This behavior slows the snake's approach or causes it to go away. A channel of communication that is specifically directed at the snake in these encounters is infrared radiation. Rattlesnakes have infrared radiation detectors on their faces (in effect, they have a pair of poor resolution auxiliary eyes, tuned specifically to electromagnetic radiation with wavelengths in the infrared range). When a California ground squirrel tail flags at a rattlesnake, a significant amount of infrared radiation glows from the tail. When the squirrel tail flags at a gopher snake (which does not have the infrared detectors) the tail remains cool[98]. Thus California ground squirrels have evolved a signal that is designed specifically to communicate with rattlesnakes.

Another example of communication with a predator occurs in Thompson's gazelles, a small antelope that lives in the grasslands of east Africa. These gazelles have many enemies, including lions, cheetahs, hyenas, and wild dogs. Some of the predators, such as lions and cheetahs, hunt by stalking. They must use cover to sneak close to a gazelle before rushing at it. A relatively short chase ensues, because the cat becomes winded if it does not catch the gazelle in the first few hundred meters. Other predators, and especially wild dogs, use a coursing pursuit. They approach the gazelles in the open, run at them, select a victim from the fleeing group, and then try to run it down in a long chase. A gazelle's escape from a stalking predator depends on sufficient acceleration and speed. Escape from coursing predators depends on speed but especially on stamina. When they are initially pursued by wild dogs, the gazelles tend to display an unusual behavior called stotting. A stotting

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[98] Rundus, A. S., Owings, D. H., Joshi, S. S., Chinn, E. & Giannini, N. 2007. Ground squirrels use an infrared signal to deter rattlesnake predation. *Proceedings of the National Academy of Sciences of the United States of America* 104, 14372-14376.

individual bounds in high, arcing leaps, landing on all four feet simultaneously before bounding upward again. Gazelles do not stott when they are pursued by a cheetah. They just stretch the neck forward, lay the ears back, and run as fast as they can. This difference, stotting when pursued by a coursing predator but not when pursed by a sprinting predator, suggested to Claire FitzGibbon that gazelles, by stotting, were signaling their physical fitness to the wild dogs. In essence, the idea is that each gazelle is trying to influence the dog's choice of a target. It is trying to get the dogs to choose another gazelle to run down. By watching wild dog hunts and measuring gazelle stotting behavior, FitzGibbon was able to make a reasonable test of this hypothesis. She found that gazelles that the dogs chose to chase tended to stott at lower rates (number of bounds per second) and for shorter durations than gazelles not chosen[99]. Coursing predators commonly appear to study fleeing prey and are reported to have an "uncanny" ability to spot subtle deficits of movement that indicate vulnerability. The stotting of gazelles probably evolved as a way to thwart this perception in wild dogs. Once started, this defensive tactic became a venue of competition among individuals in the selfish herd. So now, in a herd of gazelles chased by wild dogs, all individuals make repeated bounds high into the air, to give the visual equivalent of shouting, "NOT ME - THE OTHER GUY!" "NOT ME - THE OTHER GUY!".

Courtship

A final major category of communicative acts involves courtship. We define courtship as the behavioral signals that precede and coordinate copulation. Broadly, courtship

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[99] FitzGibbon, C. D. & Fanshawe, J. H. 1988. Stotting in Thompson's gazelles: an honest signal of condition. *Behavioral Ecology and Sociobiology* 23, 69-74.

comprises two kinds of signals. First, there are the signals that are involved in attracting a mate, as in the case of flashing by firefly males. Cricket chirping is performed by males to attract females to their burrows. The choruses of frogs that fill the nighttime air with sound in temperate and especially in tropical regions are made by collections of males at a mating site (usually a body of water). Each male frog fills his lungs and then expels air through the larynx. Vibration of the laryngal membranes produces sound, but the sound is greatly amplified by passage of the vibrating air into the male vocal sac, a thin-skinned pouch below the mouth. The vocal sac bulges out and becomes a resonating chamber. A calling frog shuttles the air back and forth between the lungs and the vocal sac with muscular contractions that consume much energy. Although most bird song acts as advertisement of territory ownership, in many species males occupy territories first and their song initially has two functions. Song helps to keep other males away, and it is broadcast to attract a female mate.

However, despite these well-known examples of acoustic advertisement for mates, the more common mate attraction signals are chemical. For example, chemical sex attractants are identified in more than 1,600 species of insects[100]. In many mammal species, females, as they approach estrus (coordinated ovulation and behavioral receptivity to copulation) release sex attractant compounds in urine, or as volatile scents from the vagina.

In all of these examples, the effects of the signals are to bring males and females of the same species together. However, mate attraction alone does not guarantee copulation. Usually

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[100] Roelofs, W. L. 1995. Chemistry of sex attraction. *Proceedings of the National Academy of Science of the United States of America* 92, 44-49.

mate attraction is followed by a further round of signaling that may include movements, sounds, and scents. The purpose of this second round of signaling is twofold. First, it is a check on species identity. One of the worst mistakes that an animal can make is to waste a reproductive opportunity by mating with an individual of another species. Second, the added round of signaling is used to evaluate the suitability or quality of a potential mate.

In long-lived animal species in which individuals mate for life (many seabirds, for example), the outcome of this second signaling round is critically important for an individual's lifetime fitness. Typically, animals with these life history characteristics have a relatively low annual reproductive output, and the one or two young from each breeding season do not always survive. To accumulate fitness, an individual must make a solid effort at reproduction each year, over many years. In seabirds, as in most birds, the hatched young have huge energy demands that can only be met by the combined efforts of both parents. So, when a young adult bird is about to commit to a pair bond with another individual, that will be its reproductive partner for perhaps 30 years, it is important to make a good choice.

An example of such a species is the Laysan Albatross. Individuals that are shopping for a mate perform an elaborate "dance" with the potential life partner. In a dance, both individuals face each other and display motor patterns that one researcher[101] named as follows: 1) bill under wing, 2) scapular action, 3) sky moo, 4) sky call, 5) air snap, 6) sky snap, 7) head flick, 8) head shake and whine, 9) stare, 10) stare and whinny, 11) rapid bill

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[101] Meseth, E. H. 1975. The dance of the Laysan Albatross. *Behaviour* 54, 217-257.

clapper, 12) eh-eh bow, 13) bob, 14) bob-strut, 15) bow-clapper, 16) bill touch. The dance is coordinated in some way, so that while one partner is performing one set of actions, the other predictably performs another set. The birds bob up and down, clap their beaks loudly, move the beak under the wing or to the back and clap the beak, shake the head, throw the beak to point vertically upward and give a call, and in summary perform a rich set of ritualized actions that are seen in no other context. Exactly what about the motions of a potential partner a birds attends to is not known, but it is common for one partner to break off and walk away. It has seen something that indicates unacceptable quality in the dance partner, and it will search for another possible mate.

Chapter Eleven

Sexual Behavior

The Northern Elephant Seal gets its name from the fleshy, pendulous snout of males, that resembles a short elephant's trunk. The snout, somewhat like the vocal sac of frogs, acts like a resonating chamber, to alter the amplitude and the frequency characteristics of male vocalizations. Males produce their very loud, breathy, flatulent vocalizations from their beachfront territories, adversing ownership in the seal equivalent of bird song.

Northern Elephant Seals spend most of their lives at sea. In the rich waters off the northwest coast of North America and up into the Gulf of Alaska, they find abundant squid, the main item in their diet. Seals are a transitional form. They are an example of a lineage that is part-way through an evolutionary transition. They are mammals that are in the process of evolving from terrestrial life to aquatic life. The whales and dolphins have made the complete transition; they spend all of their lives at sea. The seals have not made the complete transition. They cannot give birth or care for their young in the water. So all seals haul out onto land or ice to give birth to their pups and to suckle them.

Most seals, including Elephant Seals, have a postpartum estrus. They copulate and initiate a new pregnancy almost immediately after giving birth. Favorable beaches on islands where females can come ashore to give birth and not have to deal with terrestrial predators are rare. Thus, many females tend to appear at one spot. The concentration of receptive females in space and in time sets the stage for competition among males.

In Elephant Seals, as in nearly all mammals, all the expense of producing young is borne by females. Males provide only genetic material. A female grows the fertilized egg in the uterus, feeding the developing fetus directly from her own blood, and then continues to feed the young after birth in the energetically very expensive process of lactation. In mammals, females provide all the energy and materials needed to transform a fertilized egg into an independent offspring. Males simply fertilize the egg. Thus, a male's lifetime reproductive success is determined solely by the number of eggs that the fertilizes, that is, the number of sexually receptive females with which he copulates. A male can elevate the number of copulations that he achieves in two ways: he can attempt to sequester females and he can attempt to keep other males away from them.

Elephant Seal males strive for these goals by arriving early on the island beaches where the females later will come ashore. Mature males set up territories right at the water's edge, so they can intercept and corral females as they come out of the surf. Each male with one of these beachfront territories assembles a harem of several dozen females. A female finds these males useful because they defend a territory where the female can give birth in relative peace, not bothered by throngs of suitors. Males defend their territorial boundaries from neighboring males and from younger males that attempt to enter. A male's defense of his territory involves guttural song, threat postures, and fighting. Fighting males rear up facing each other and slash downward at the opponent's face and neck with powerful canine teeth. Although males have specially thickened and calloused skin in these areas, they still become cut. Two adversaries in a prolonged fight will have blood streaming down their necks. The fighting blows are also a kind of clubbing, in which the force of each male's mass is brought downward on the opponent. Because body mass in part determines the outcome of these fights, mature males are large. Body length is about five meters and body mass is about 3,000 kilograms. Female body length is about three meters and body mass is about 900 kilograms.

A mature male is about three times the size of a mature female for one reason. Male size determines the outcome of fights, and fights determine whether males retain territories and get to copulate. The utter dependence of male reproductive success on male mating success also is the reason for the male proboscis and the vocalizations that it helps to make, for male territoriality and defense of females, for male pugnacity and willingness to fight, and for complete disregard for the welfare of pups or the mating preferences of females. When a male, resting near the center of his territory, detects another male encroaching on his territory boundary, he runs, as best as a three ton animal that is designed for swimming can run, toward the intruder. A running seal flexes its spine up and down to throw its body into rippling waves and it flows across the ground, using its flippers for support. As the territorial male charges toward the intruder, females that are in his way scatter and are thrown to the side. The male simply runs over small pups that are unlucky enough to be in his path. Under his crushing weight, they are injured and quite often killed. When a male detects, by odor, a postpartum estrus in one of the females in his harem, he lays across the female, pinning her to the ground with his 3 ton weight while he probes to insert his penis. The female cannot get away. Her only option in this situation, if she finds the male to be an unacceptable mate, is to give a protest vocalization, which may draw in other males, forcing the male on top of her to get off and fight.

Sexual Selection

The evolutionary process by which sex differences in body size and behavior come about in Elephant Seals is called sexual selection. Charles Darwin coined the term in his first book[102]. In this book, Darwin presented and evaluated the idea that the principal cause of evolutionary change in species was natural selection. As I described in Chapter One, natural selection occurs when individuals vary in a trait, when variation in the trait is linked to individual differences in lifetime reproduction, and when the trait has a significant heritability. Natural selection is the process by which species change genetically to become increasingly better fitted to their environments. In *Origin*, Darwin thoroughly considered all the possible challenges to his theory. One obvious challenge is that in many animal species, males and females differ in aspects other than their genitalia. Within a species, males often are larger than females, they possess odd structures such as the Elephant Seal proboscis, or the horns and antlers of most hoofed mammals, and they are easily motivated to fight. How can it be, Darwin realized, if the environment defines a single best optimum for a species, a form and function that makes individuals as good as possible at survival, growth and reproduction, that different forms, male and female, come about? If a body mass of 900 kilograms is best for a female Elephant Seal to gather resources and to convert these into offspring, why should males be three times larger?

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[102] Darwin, C. 1859. On the Origin of Species by Means of Natural Selection, or the Preservation of Favoured Races in the Struggle for Life. John Murray, London.

Darwin concluded that there must be a process other than natural selection that pushed males to evolve larger body size, weapons, and pugnacious dispositions. Darwin called this process sexual selection. He proposed that, because mating is a crucial required step in sexual reproduction, characteristics with the sole purpose of making individuals more successful at mating could evolve to extremes that were opposed by natural selection. Eventually, some equilibrium is reached at which the fitness advantages of an extreme trait that creates greater mating success is offset by the survival costs of the extreme trait. Thus, in most species, we view the female condition as the optimum that is defined by the environment, and the male condition as somewhere off that optimum. The distance that males are away from the environmental optimum will be set by the importance of male mating success for male reproductive success.

Polygyny

Another characteristic of species, like Elephant Seals, in which males are specialized to compete for matings, is substantial variance in male fitness. In a typical year, most breeding age males do not reproduce, and within the small fraction of males that do reproduce, there is pronounced skew: there are a few males that sire many offspring, and many others that sire only one or two. In contrast, just about every female mates, and in the subsequent year gives birth to a pup. Thus, although the average reproductive success of males and females is equal (it has to be: one male and one female are needed to make each pup), the variance in male reproductive success is large and the variance in female reproductive success is small. This condition, where variance in male reproductive success greater than variance in female reproductive success, is called polygyny.

When there is polygyny, males tend to be larger than females, they tend to have weapons of some sort and the behavior to aggressively use the weapons. They employ various ways, including territoriality, to establish harems, groups of females that they attempt to hold together and defend against other males. They are behaviorally focused on copulation and they do not form pair bonds with females. They are indifferent to juveniles, as is true for Elephant Seal males, or they practice infanticide, as is found in species such as langurs or lions, where there is turnover of single males that defend female groups. When females mate more than one time per receptive period, males have adaptations to deal with sperm competition. Sperm competition refers to the fact that reproductive competition among males may not end at copulation. Until an egg is fertilized, there is the opportunity for one male to displace another.

Male adaptations to deal with sperm competition are quite varied. In some species, males practice mate guarding after they copulate. They hover close to the female and do not permit her to go out of sight until enough time has passed to ensure fertilization. In other species, males insist on frequent copulation. For example, in the giant water bug, *Abedus herberti*, a male copulates with a female and then permits her to lay eggs on his back. The eggs come with a sticky glue and thus the male will carry them until they hatch. While the eggs are developing, the male does not feed, and he moves in specialized rocking motions to ensure proper aeration of the eggs. Females may mate with several males, and thus a male is at risk of accepting and caring for eggs that he did not fertilize. Experiments in the laboratory showed that there is a strong last-male bias. That is, when a female has mated several times, the next egg that she lays is usually fertilized by the male that mated with her most recently. Because of these characteristics, male giant water bugs insist on frequent copulation. They allow a female to glue no more than three eggs to their backs before requiring another copulation[103]. In one recorded instance, a pair of bugs took 36 hours to transfer 144 eggs to a male's back, and during this interval, copulated over 100 times. In other insect species, male genitalia come equipped with structures that act like scoops, to remove another male's sperm. Similar flushing techniques are known in some birds and mammals. Male seminal fluid may contain compounds that, in the vagina, set up like glue, forming a rubbery plug that blocks additional sperm. In other species, seminal fluid contains compounds that are toxic to subsequent sperm. Finally, males often compete by the number of sperm that they ejaculate. Suppose that two males mate with a female, and one male ejaculates 200 million sperm, and the other male 800 million. If there are no other sperm competition mechanisms operating, then the second male will fertilize 80% of the eggs. For this reason, males in polygynous species often have vary large testes, ejaculate prodigious numbers of sperm, and can do so repeatedly, with short refractory periods.

Another evolutionary consequence of polygyny is the existence of alternative reproductive tactics in males. The most common alternative reproductive tactic is one that is generally described as "sneaker." For example, most species of salmon have an alternative male form,

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[103] Smith, R. L. 1979. Repeated copulation and sperm precedence: paternity assurance for a male brooding water bug. *Science*, 205, 1029-1031.

called a Jack, that is a sneaker. Recall my brief mention of the salmon mating system in Chapter Six. Most male and female salmon have spent two to several years at sea, feeding and accumulating the resources needed for a single massive bout of reproduction. At the spawning site, females dig shallow nests in the gravel to receive their eggs. Males defend these sites and the females with threat postures and fighting. Males are larger than females, and in preparation for fighting, their jaws have developed into an enlarged, hooked shape that resembles tin snips. The genus name of the Pacific salmon, *Oncorhynchus,* means hooked nose. A male aggressively defends a female until she lays her eggs. He hovers close to her as she adopts the oviposition posture, and when she releases her eggs into the nest, the male immediately covers them with a cloud of sperm. As in Elephant Seals, the success of a one of these hook nose males is related to his size, strength, vigor, and fighting ability. While the fish were at sea, females were amassing the resources needed to produce as many high quality eggs as possible. Males were amassing the resources that would allow them, during the upstream migration, to transform themselves into big, lethal fighting machines with huge testes. The alternative male type, the Jack, does not stay at sea several years; Jacks return to the natal area after one year. A Jack is small, and it does not have the red color or the tin snip snout of hook nose males. A Jack does not participate in the fights among males for ownership of a female and her nests. Instead, he lurks, usually in vegetation, close to a female and the hook nose male that is defending her. At the instant that the female releases her eggs, the Jack darts in quickly and deposits his sperm on them. Then he darts away, trying to avoid the slashing jaws of the big hook nose male.

The Jack strategy in salmon has frequency-dependent success. That is, the average fitness of the Jack strategy is dependent on how frequent Jacks are. By frequency we mean the proportion of the total male population that Jacks make up. When almost all males are the hook nose form, then a rare Jack can be very successful. Then, as Jacks become more common, competition for the weedy sites where they lurk goes up, and they are more easily detected and attacked by hook nose males.

How does a young male make the "decision" to become a Jack or a hook nose? The answer seems to be growth rate. When he is a smolt, if a male is healthy and growing fast, he is more likely to become a Jack. At any given smolt age, a male that is smaller tends to choose to stay longer at sea and to return as a hook nose[104]. These findings contradict the commonly held notion that the "sneaker" strategy represents the best option for a male in a compromised situation. In salmon, Jacks are probably the higher quality individuals, and some recent evidence suggests that the behavior of spawning females is designed to favor fertilization of their eggs by Jacks[105].

Monogamy

In most species of mammals, the mating system is polygyny. This is because, as I noted earlier, of the extreme asymmetry in parental expenditure in offspring that exists in mammals. Females provide all the energy and materials that are needed to produce an

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[104] Gross, M. R. 1991. Salmon breeding behavior and life history evolution in changing environments. *Ecology*, 72, 1180-1186.

[105] Watters, J. V. 2005. Can the alternative male tactics "fighter" and "sneaker" be considered "coercer" and "cooperator" in coho salmon? *Animal Behavior*, 70, 1055-1062.

independent offspring, and thus they are in effect a resource that males compete for. Given the absence of any kind of significant male expenditure in offspring, males become specialized at competing for matings.

In other animal groups, in which males put some energy into rearing offspring, what looks like monogamy is common. For example, most bird species appear to be monogamous, because the efforts of both parents are required to raise a brood. Two kinds of parental effort are needed in birds. First, the eggs must be incubated. They must be kept warm and nearly always, this occurs by a parent sitting on them. Obviously, while you are sitting on eggs, you can't search for food, so constant incubation means either that the parents must take turns, or that one parent must feed the other. Then, after the eggs hatch, the energy demands of the chicks are gargantuan. The gaping chick beaks have to be stuffed with high quality food at very frequent intervals. Ornithologists who have hand-reared bird chicks in the laboratory testify that it is remarkably exhausting, and they usually vow never to do so again. Baby birds have huge energy demands because, first, they are endothermic (warm blooded). Like mammals, they maintain a high and constant body temperature. Because they are small and lightly feathered, they must burn energy at a great rate just to produce enough heat to maintain body temperature. Second, birds have very fast growth rates, which create another insatiable demand for energy. In most bird species, the efforts of two parents, working from sunup to sundown every day, are required to deliver enough food to bring the chicks to fledging. Fledging is the point at which juveniles can fly from the nest and start to feed themselves.

Thus, in most bird species, individual males and females pair off. There is a courtship phase, which may be lengthy, in which the two birds in effect agree to be reproductive partners. Both birds may help to build the nest. Quite often, both defend the territory boundaries. They copulate. The female lays eggs in the nest. Cooperative incubation and continued territory defense occur. They eggs hatch, and now the parents either guard the nest and the nestlings, or they forage, to ferry an unending supply of food into the mouths of the hungry chicks.

The reproductive biology of birds thus seems to require monogamy - equal variance in the reproductive success of males and females - because all males and females are members of a mated pair. This was the consensus among ornithologists until the 1990s, when DNA technology progressed to the point at which genetic assignment of paternity became relatively easy. Then, in species after species, the shocking news came out that the chicks in the nest often were not fathered by the social mate, the male working hard to do all that feeding. They were fathered by the male in a nearby territory. Ornithologists were forced to conclude that in the monogamous birds, many Extra-Pair Copulations (EPC) were happening. This was a shock because when you watch members of a mated pair in nature, you do not see these copulations (you rarely if ever see any copulations). However, in some species, EPC rates are so high that all the chicks that a male cares for in his nest are not his own. EPC is the rule, rather than the exception, in birds and biologists now make a distinction between social monogamy and genetic monogamy. Most birds are socially, but not genetically monogamous, and the EPC occur surreptitiously.

Why birds act this way is not entirely clear at present. It is relatively easy to see why a male might engage in EPC. If he can take a moment out of his busy foraging day for a quick copulation with the female next door, he can cheaply increase his fitness without having to care for those additional chicks that he has fathered. Also, EPC are available before egg laying, and because all birds in a neighborhood are synchronized, EPC usually are available before a male has his own chicks to feed. However, the more time that a male spends out looking for EPC, the less time he can devote to monitoring his mate, and thus the greater his risk that she will have EPC with a neighboring male. At least for males, we can estimate a balance between EPC and mate guarding that maximizes fitness. However, in most species, what advantage females get from EPC is not that obvious. Researchers have proposed many hypotheses, but at present, there is not a conclusive answer.

Sexual Conflict

An adult man crouches in the bushes and watches two small brown birds through binoculars. The female bird crouches, elevates her tail, and partly everts her cloaca. The male bird pecks at the opening of the cloaca. The female bobs her rump downward a few times, deposits feces, and then a small clear droplet. The male bird peers briefly at the droplet and then the two birds quickly copulate and fly away. The man, who watched these events intently, crawls on his hands and knees toward the spot where the birds stood, and is thrilled when he sees the droplet on a small stone. He carefully collects the droplet and rushes away in great excitement.

This man, who to a casual observer would appear deranged, was the biologist Nick Davies, who studied the reproductive behavior of dunnocks (*Prunella modularis*), a small secretive brown bird, in the Cambridge University Botanic Garden. Davies was pursuing the question of why this species appears to show so much variability in its mating system. In the population that Davies studied, males and females independently defended territories, with varying amounts of overlap. On some territories, a single male and female practiced typical birdlike social monogamy. On other territories, a single male's territory overlapped with those of two females, and the male appeared to be mated with two females. On other territories, a single female was associated with two males. Finally, some territories had messy arrangements with two or more females and two or more males.

By monitoring the rates at which adults fed nestlings, and recording the fates (survive or die) of nestlings, Davies found that the sexes differed in what was optimal for reproductive success[106]. For individual males, the greatest number of offspring fledged per season came about under polygyny, where a single male mated with two females and helped both to rear the chicks. For a female, this arrangement was not optimal, because she did not have the male's undivided feeding efforts and so the survival of her own chicks was diminished. A female had the greatest reproductive success when she was associated with two males, that both fed the chicks. However, a male will feed a female's chicks only if he has copulated with that female several times, and thus has a reasonable chance of paternity. So a female with two males on her territory needs to copulate with both to be sure that both will feed the chicks. However, males also practice mate guarding, so the females are required to be

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[106] Davies, N. B. 1992. Dunnock Behaviour and Social Evolution. Oxford University Press, Oxford.

quick and sneaky about soliciting copulations from male number 2. If male number 1 sees his female copulating with male number 2, he becomes less likely to feed the chicks.

A female in association with two males does best if she can elicit the services of both to feed the chicks, but the males try to evict each other, tend to suspend chick feeding if they do not get to copulate or if they see the female copulate with the other male, and tend to insist on cloaca pecking, which causes the female to eject a droplet of the other male's sperm. When a male has two females on his territory, the females are hostile to each other, may interfere with each other's nests, and neither female gets the male's complete chick feeding performance. Each sex would in effect like to have the exclusive reproductive services of two members of the opposite sex, and individuals of each sex attempt to prevent this from happening to themselves. These characteristics, in which the optimum conditions for the sexes are in opposition, is called sexual conflict.

Quite a few reports of sexual conflict appear in the scientific literature. The grisly phenomenon of infanticide provides a particularly clear example. In Chapter Three, I explained how infant killing by adult males is a reproductive adaptation. Infanticide is most common when groups of females are defended by a single male that periodically is ousted by another male. The new male that takes over control of a group can increase his fitness by killing the offspring of the rival that he just deposed, and by mating as quickly as possible with all females in the group. Infant killing upon group takeover accomplishes both of these goals. However, the female whose infant is killed does not benefit. The death of her infant is a fitness loss for her. The sexes are in fundamental conflict, and the evolutionary consequences of the conflict ripple outward. For example, infanticide following male takeover occurs in lions. The average size of groups of female lions, by some estimates, is larger than what is currently best to maximize the per capita intake rate of prey. Some researchers have proposed that these larger than optimal group sizes have evolved as a response to infanticide, because several females can cooperatively threaten a male away from a cub that he is trying to kill.

Infanticide is a heart-rending adaptation, and it is an example of the fact that the effects of natural and sexual selection are not beneficent. Selection is indifferent to everything except fitness, and so behavior that seems horrible to us can evolve. In other instances, the behavior that evolves out of sexual conflict is more similar to Shakespearian comedy. One of my favorite examples occurs in a species of burying beetle. The burying beetles are a group of about 70 species that are specialists at using vertebrate (mostly mammal) carcasses as a reproductive resource. Big carcasses in nature (such as a dead mouse or rat) are very valuable sources of energy, and many life forms, including bacteria, fungi, insects, and other vertebrates, are adapted to exploit them. To save a carcass for their own reproductive purposes, a pair of beetles digs beneath it, covers it with soil, clips off all the hair, treats the shaved surface with oral and anal secretions that soften the carcass and protect it from microbial attack, and mold it into a rough sphere. Now the beetles have a rich ball of energy hidden in an underground brood chamber. The female lays her eggs and the larvae, when they hatch, feed from an opening in the carcass that the parents have prepared, or the parents regurgitate partially liquified carcass material to them. Burying beetles are rare among insects in the elaborate parental behavior shown by a breeding pair.

When a single beetle finds a carcass, he or she releases a pheromone that attracts a beetle of the opposite sex. Two partners are needed to quickly bury the find, as well as to produce fertilized eggs. If more than one male is drawn to the carcass, then the males fight violently until a single winner drives the other males away. Likewise, females attack and attempt to evict other females that show up. If the carcass is large enough, more than one female can rear a brood on it, but only at diminished output per individual. A female can rear more young if she is not forced to share. Here is where sexual conflict becomes apparent. A male will have higher reproductive success if two or three females come to the carcass. He can sire all the broods and collectively produce more offspring than if he remained monogamous. On a small carcass, that can support only one brood, a male does remain monogamous. On a large carcass, the male tries to release the attractant pheromone, to draw in additional females. The female in the pair has a fitness interest in not allowing the male to advertise for more females.

This is the arena for sexual conflict in the burying beetle *Nicrophorus defodiens*, that Anne-Katrin Eggert and Scott Sakaluk studied[107]. In this species, males attempt to attract additional females by mounting an elevated spot, then performing a kind of head stand. The head stand posture exposes the terminal abdominal segment, from which pheromone

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[107] Eggert, A.- K. & Sakaluk, S.K. 1995. Female-coerced monogamy in burying beetles. *Behavioral Ecology & Sociobiology 37: 147-153.*

is released. Females try to stop or prevent their mates from doing this by biting them, knocking them off balance, or by jumping onto the male's back.

Figure 11.1 - A male burying beetle on the right is trying to adopt the head stand posture to release attractant pheromone that will draw in new females. His mate, on the left, has jumped on his back to prevent this. The male is trying to kick her off. Photograph by Anne-Katrin Eggert.

Eggert and Sakaluk decided to measure the effectiveness of these female countermeasures in the laboratory, where pairs were presented with a rat carcass. To prevent the female from resisting advertisement by her mate, the researchers tied a tether of dental floss around the female's waist, so that she could move around the carcass, but not get off it. In the cage with the carcass, the researchers also provided a small rock that the tethered female could not reach. Then they measured how often the male managed to get into his head stand position and how long he was able to remain in that position, when his mate was tethered, and when she was not. The results? With his mate unable to follow him to the little rock, the male spent significantly more time with his butt in the air, wafting his come-hither-baby pheromone.

Female Choice

In his original presentation of the idea of sexual selection, Darwin intended to explain two kinds of traits that we see in nature. The first kind, as I have described, is that males tend to be larger than females, to have weapons that females do not, and to be more likely to fight. These characteristics, as Darwin realized, are explainable by the central role of mating in male reproduction. Males evolve large size, weapons, and pugnacity because these traits give them an advantage in competing against other males for mating opportunities. The other way in which males sometimes differ from females is less easily explained. In some species, and especially in birds, males are ornamented. The male ornaments include bright, conspicuous colors and often extremely exaggerated structures. For example in the Marvelous Spatuletail Hummingbird, *Loddigesia mirabilis,* the male, like most male hummingbirds, has a gorget, throat feathers that are specially modified to refract light to produce brilliant, intense color. The male Spatuletail is unique, however, in its highly modified tail feathers. The tail contains just four feathers, and two of these are extremely long (longer than the bird's body) bare shafts that are tipped with a circular blue discs.

Figure 11.2 - A male Spatuletail Hummingbird. Photograph by Bernardo Roca-Rey Ross.

Ornaments like this cannot be explained as traits that help males to threaten or to hurt each other, and they certainly don't seem designed to help survival, so how do they come about? Darwin thought of an explanation and in doing so displayed his astounding mind as well as his intellectual freedom from the *zeitgeist.* Darwin proposed that the ornaments evolved to such extremes because they made the males more attractive to females. In other words, the ornaments evolved through the actions of female mate choice. In mid-nineteenth-century England, this was a bold, radical idea, almost as radical as Darwin's assertion that species are not immutable.

Darwin's idea that the actions of females might count for something was so ahead of its time that it did not receive any serious thought from biologists until about 70 years later. Even then, biological theoreticians developed only one-half of the hypothesis. Darwin's hypothesis contains two big ideas. The first, somewhat lesser one, is that ornaments, where they exist, might influence male mating success. The second, more important, idea is that the actions of females can determine the outcome of competition among males. Although Darwin, and most of the theoretical biologists who took up his hypothesis, were looking for an evolutionary explanation for male ornaments, the crucial idea, that females might have agency, was in print. More than 100 years passed before someone realized the more general significance of Darwin's idea. That person was Robert Trivers, who noted that whenever there is asymmetry in parental expenditure, where one sex spends more time, risk, or energy on offspring than the other sex, then the sex with the greater expenditure is expected to evolve choice behavior[108]. In most animals, females make the greater expenditure, so they should be the choosy sex. What should females choose? Either they should choose the male that offers the best resources (for example, territory quality, or an actual food gift), or they should choose the male that offers the best genetic material for offspring. The importance of Trivers' idea is that it predicts where we should expect to see well developed female choice, irrespective of ornaments. Although Darwin was trying

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[108] Trivers, R. L. 1972. Parental investment and sexual selection. In: *Sexual Selection and the Descent of Man, 1871-1971* (Ed. by B. G. Campbell), pp. 136-179. Aldine Press, Chicago.

to explain ornaments, an ostensible contradiction to his theory of natural selection, he came up with a much bigger idea. It only took biologists 110 years to see it.

We now know that female mate choice, especially in species, as Trivers predicted, where females spend much more on offspring than males do, is common. The mate choice often involves a kind of sampling period, in which the female appears to be comparing potential mates in some way. This is most obvious on leks, where a female can easily move among male territories, and the only purpose of her visit is to find a mate.

For example, in the high sagebrush deserts of North America, male sage grouse defend small territories (no more that about 2-6 meters in diameter) that are clustered together in clumps of several dozen. At dawn, each male begins to display on his little territory. Females fly in to the vicinity of the lek, then walk among the territories, apparently assessing potential mates. Eventually, the female chooses a male, mates with him, and then flies away, to build a nest and to incubate eggs on her own.

On each territory that she visits, the female is greeted by a male that approaches and displays to her. The principal basis for each male's display is his esophageal sac, which sits in a muscular bag that hangs like a heavy shawl draped across his chest. The sac is an outgrowth of the esophagus and it is large, compared to the size of the bird. Its internal volume is 4-5 liters. To display, a male erects his pointy pail feathers in a fan that frames his head and the esophageal sac, which is covered with brilliant white feathers. The male raises and lowers the pouch twice in gulping motions that shuttle air from the lungs upward and into the pouch. He produces three soft coos and then, with obvious exertion, contracts the muscular bag around the pouch, pressing it backward into the spine. Then he abruptly relaxes the contraction. The bag swells forward, and two pale featherless patches of skin on the front of the pouch bulge outward briefly. Concurrent with this motion is the culminating sound of the display, described as *poink*. The *poink* is a composite sound. There are two snaps, produced by the collapsing air sac, spaced at about 2-tenths of a second apart. Between the snaps the male uses his syrinx to produce a frequency-modulated (the sound frequency rises, then falls) whistle. Sound energy from the snaps tends to project forward and sound energy from the whistle is distinctly beamed to the right and left. The human ear simply hears *poink*, but one researcher noted that the effect of the whistle was to make the sound have a more "mellow" quality[109].

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[109] Wiley, R. H. 1973. The strut display of male sage grouse: a "fixed" action pattern. *Behaviour* 47, 129-152.

Figure 11.3. A male Sage Grouse at the moment that the strut display produces the *poink*. Photo by Gail Patricelli

For males, the act of inflating the huge air bags, compressing them violently, and then abruptly releasing the pressure looks taxing. A male performs this display many times in quick succession, especially when a female enters his territory. A male that attracts many females may display at close to 1,000 times per day, essentially doubling his daily energy expenditure[110]. Males that display at these high rates loose mass and they are forced, when they take a feeding break off the lek, to travel greater distances to find high quality food.

On a lek, there is pronounced skew in male mating success. A few males are very popular, and attract and mate with many females, and most males have more limited or no success. When researchers have measured different aspects of males to see what characteristics predict mating success, they found that no physical measurements seemed important. Rather, it was a particular aspect of the display motion itself, the time interval between the first and second snaps that make up the *poink*, that predicted male mating success. What information is conveyed in such tiny time differences is unclear at this point, but it seems that females are attending to some aspect of the display that indicates a male's proficiency in motor performance. That is, females are paying attention to male motor skill. In addition, because the displays are so energetically expensive, the females may be measuring, by a male's display rate, his overall vigor.

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[110] Vehrencamp, S. L., Branbury, J. W. & Gibson, R. M. 1989. The energetic cost of display in male sage grouse. *Animal Behaviour* 38, 885-896.

These two aspects of males, vigor and skill, make sense as traits that a female, looking for good genes for her offspring, should pay attention to. Vigor, the ability to perform energetically expensive acts repeatedly, and skill, the ability to perform physically challenging motor acts well, are likely to be accurate predictors of overall organism performance. Probably, vigor and skill reflect an individual male's genetic load, the number of small effect deleterious mutations that he carries. Small effect deleterious mutations are common in animal genomes, and they tend to build up in numbers because, individually, they are weakly opposed by natural selection. The fewer the number of small effect deleterious mutations that a male carries, the greater the likelihood that he will be able to preform with the consummate athletic grace that nature demands. A female that can detect subtle differences in male motor performance can, in a way, peer into the complete genomes of potential mates. An increasing number of studies are finding that male mating display involves skilled athletic performance, and that females seem to base their mate choice decisions on their evaluations of such performance. It may be that the ornaments that troubled Darwin so much evolved, in the few species that do have ornaments, as tricks, as secondary enhancers designed to improve the apparent quality of male motor performance[111].

Male weapons, large body size, aggressive display, and fighting are dramatic and easy to observe. Female choice is more subtle, and this may be one reason why it was ignored for so long. However, the evolutionary consequences of female mate choice are certainly as

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[111] Byers, J., Hebets, E., & Podos, J. 2010. Female mate choice based upon male motor performance. *Animal Behaviour* 79, 771-778.

comprehensive as the consequences of aggressive competition among males. The full scope of female mate choice remains unknown.

Chapter Twelve

Humans

Through the filters of natural selection and sexual selection, animal species become increasingly perfected, so that individuals behave as if they are constantly asking themselves the question, "What should I be doing at this moment to maximize my inclusive fitness?". As you have read in this book, there are many examples that display animals behaving in ways that seem as close to perfect as possible to achieve fitness goals. However, there are also examples of behavior that does not completely match the current environment. For example, the species that I study, the American Pronghorn, is extremely accomplished at running. Individuals can sprint at speeds close to 100 kph, and they can run in a smooth relaxed gait at 60 kph for several miles. They are masters of speed and of distance running and their abilities far outstrip those of their current would-be predator, the coyote. When pronghorn are pursued and frightened by humans on machines, they bunch into a tightly packed ball that flows smoothly over the ground. The ball flows smoothly because individuals synchronize their movements. Pronghorn have three high speed gaits. A gait (trot versus canter, for example) is defined by the sequence in which each of the four feet touch the ground and by the temporal position of suspension phases, moments when all feet are off the ground. Within a running herd of pronghorn, there is nearly perfect uniformity in the gait being used. There is also nearly perfect agreement in the lead foot (the first foot to strike the ground in a gait cycle) used. A running group can switch from one gait to another while preserving the synchrony of the lead foot.

This kind of advanced running ability is far more than what is needed to deal with coyotes or even wolves. So why are pronghorn so over built? There is no need to be three times faster than a current predator, so why not use the resources that go into building all that excess speed to do something that makes a useful contribution to fitness? The answer to this question is that the environment that pronghorn occupy today is very different from the environment that they occupied a short time ago. For most of the past 5 million years, pronghorn occupied the vast grasslands of North America. They shared that grassland with a rich diversity of other herbivore species and with an equally diverse group of predators, including lions, hyenas, fast-running giant bears, and big cheetahs. For most of their evolutionary history, pronghorn were pursued by sprinting, stalking, and coursing predators, and they evolved running talents that were commensurate with those multifaceted risks. Then, about 10,000 years ago, the end-Pleistocene extinction event wiped out most of the diverse North American fauna: most of the herbivores and nearly all the carnivores disappeared. Pronghorn came through the extinction event along with two lesser predators, coyotes and wolves, for which they are drastically overbuilt. Pronghorn have extreme running ability because of their recent evolutionary past, not because of the present.

Pronghorn also have a strong grouping tendency, even though a selfish herd survival advantage does not currently exist. Within groups, pronghorn have very high rates of dominance interactions, which tend to push subordinate individuals toward the periphery of groups. In the present, there is no fitness cost of being on the outside edge of a group, but there would have been such a cost in the recent past, when lions, hyenas, and cheetahs were present.

After I discovered the early experience effects on the acquisition of social rank in pronghorn, that I described in Chapter Nine, I followed marked individuals throughout their lives, to gauge how strong and persistent the early experience effect was. I found that individuals retain the social rank that they acquire when they are fawns. I also made a number of different measures of fitness and I could find no fitness consequences of social rank. Very low ranking individuals had feeding rates, survival, and lifetime reproductive success that were equal to those of very high ranking individuals[112]. Thus, pronghorn fight for early dominance status, have many dominance interactions per day, retain status throughout life, but gain absolutely no fitness advantage from all the effort. Social dominance behavior, like running ability, exists because of evolutionary lag, because the environment for pronghorn changed only recently, and not enough time has passed for natural selection to adjust their behavior or anatomy.

Now, reader, can you think of another species for which the idea of evolutionary lag in behavior and anatomy might apply? Can you think of another species that currently lives in an environment that is distinctly different from the environment in which it evolved and to which it is adapted? At the moment, you are probably sitting in a building, and you are probably wearing clothes. Those two aspects of technology, buildings and clothes, help to

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[112] Byers, J. A. 1997. American Pronghorn. Social Adaptations and the Ghosts of Predators Past. University of Chicago Press, Chicago.

maintain a warm, moist tropical environment immediately around your mostly hairless skin. You are a tropical creature, and only technology allows you to live outside the tropics.

Humans are apes. They are one species of four that diverged from each other in recent evolutionary time. The other three species are Gorillas, Chimpanzees, and Bonobos. We are most closely related to chimpanzees, with about 99% DNA sequence identity. The last common ancestor between humans and chimpanzees occurred about 6-7 million years ago, when the populations of apes that would give rise to humans began to de-emphasize life in the trees and to specialize on hunting and scavenging meat and gathering plant food in the emerging savannah grasslands of east Africa. Although fossils of terrestrial apes tend to be rare, concerted paleontological work has produced enough fossil material to provide a good general picture of evolution in the human lineages following the split from the chimpanzee line.

Bipedal locomotion, the most dramatic and pivotal behavioral difference that characterizes humans, appears quite early. In most physical respects, humans are fairly unimpressive. Compared to our chimpanzee cousins, we are scrawny and weak. However, in one arena, our physical performance is quite good. That arena is endurance running. As the ancestors of humans remodeled the pelvis, vertebral column, the knee, and the foot to accommodate bipedal locomotion, they also increased the length of the hind limbs (the legs). That change allows humans to adjust running speed, without significantly changing the energy cost of locomotion, by simply increasing stride length. Many other aspects of the human muscular and skeletal systems are best interpreted as modifications to enhance the efficiency of endurance running[113]. Specialization for endurance running is why humans have scrawny upper bodies and big butts. A lightweight upper body enhances energy efficiency during running, and the large gluteus maximus muscle, relatively inactive during standing or walking, becomes active during running, to stabilize the tilt of the upper body as it leans forward.

Why did humans evolve to become endurance running specialists? There are two hypotheses. The first is that endurance running evolved as a hunting adaptation. If you simply run at an aerobic pace toward an antelope, it will run away, perhaps for 500 meters, and then it will stop to observe you. As you draw near again the antelope will run again. If you can persist in this steady pursuit for several hours, then you will deprive the antelope of any opportunity to feed or to rest. Eventually, the antelope's flight distance (the distance from you at which it runs away) will begin to decrease. Eventually, you will be within a stone's throw of the antelope. This is where the persistence hunting hypothesis gets a bit weak. To eat the antelope, you somehow need to close that final 5 meter gap and, if you can do this, you need to have some way to kill the animal. It is difficult to imagine how any of the early *Australopithecus* species, that were bipedal, but small, and with no evidence of tool use, could have made the kill. The alternate hypothesis is that endurance running evolved to serve scavenging: picking up bits of carcasses left by other predators. To find carcasses and to get to them quickly, before other scavengers, humans would need to be able to patrol huge areas efficiently. Endurance running would permit this.

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[113] Bramble, D. M. & Lieberman, D. E. 2004. Endurance running and the evolution of Homo. *Nature* 432, 345-252.

Apes in the human line had become efficient bipedal running specialists by about 1.8 million years ago. From that time until the appearance of anatomically modern humans in Africa at about 150,000 years ago, brain size doubled, by a seemingly steady linear increase over a relatively short (1.7 million years) time. Many hypotheses to explain the evolution of the extraordinarily large human brain exist, and none have conclusive evidence. Anatomically modern humans dispersed out of Africa into Europe, across Asia, and into North and South America, at about 40,000 years ago. Clear evidence for human agriculture, the domestication and husbandry of plants and animals to provide an abundant, conveniently controlled, steady food supply, does not appear in archeological sites until about 10,000 years before the present. Before that time, throughout the evolutionary history from early hominids to modern humans, all evidence points to a social organization that revolved around small multifamily groups which practiced a hunting and gathering economy, defended territories, and were hostile toward other groups. Thus, humans in the present are like pronghorn, living in an environment that is very different from the one in which they evolved. To generate hypotheses that explain human perceptions, cognitive skills, and emotional responses to social situations, the starting assumption should be that the particular behavior that one wants to explain is designed to promote individual fitness in a tribal, hunting and gathering society. Biologists and some Psychologists recognized this explicitly starting only about 20 years ago. This new discipline, that seeks to understand human behavior from a biological perspective, is called Evolutionary Psychology.

At this point, you may be hitting the mental brakes. You may be unwilling to follow the line of analysis that I am developing because of your rich consciousness. That consciousness seems to be an omniscient executive that directs everything that you do. Evolutionary adaptation as an explanation of your behavior may seem irrelevant to you. I have two arguments against your objection. First, your conscious experience is produced by your brain, which is a product of evolution. Consciousness is just one of many different functions that your brain performs, and there is no known biological reason to suppose that this particular function would not have evolved in the service of maximizing fitness. Second, consider behavior that you perform without conscious control. You withdraw your hand from a hot surface before you are consciously aware of the heat. You blink when an object rapidly approaches your face. You breathe. You shiver when you are too cold. Your muscles of facial expression contract to indicate disgust when a partly liquified decomposing rat is placed in front of you. As I described in Chapter Two, your eyes almost constantly move in saccades, tiny very rapid motions that jitter the fovea from spot to spot. You yawn, sneeze, cough. When you go for a walk around the block, you do not consciously direct the movements of your legs and feet. A walking motor program does that. Similarly, your consciousness does not produce emotions. Anger, sadness, fear, shame, and joy are started in brain areas below consciousness. They trigger specific physiological responses and only sometime later are reported to consciousness. The emotion of fear is started when you perceive that you are in danger, and the physiological suite of events known as the stress response is turned on. The stress response is principally orchestrated by the hormones adrenaline and noradrenaline, which are released by the adrenal glands in response to nerve signals from the brain. These hormones increase heart rate and breathing rate, shut down digestion, increase blood pressure, and in summary prepare the body for vigorous muscular effort. Sometime after these events begin, you experience the conscious awareness of fear. The fact that an emotion starts before the consciousness of the emotion indicates that much processing and interpretation of perception goes on in the unconscious brain. Emotional states also influence conscious perception. An emotion may facilitate or may hinder your ability to perceive an environmental event.

Finally, there is now active investigation on the question of whether consciousness initiates any behavior at all. For example, consider the results of a frequently cited study conducted in the laboratory of the late Benjamin Libet[114]. The experimental subject sits with his hands resting on a table. In front of him is a clock face on which a single hand makes a full revolution every two and one-half seconds. The subject is told to flex his wrist (raise the palm off the table) at any time of his choosing and is asked to note the position of the clock hand when he makes the conscious decision to move. The subject also reports the time at which he perceives that his hand has started to move. Simultaneously, the researchers recorded EMG from the wrist flexor muscles, and with electrodes placed on the scalp, recorded the readiness potential. The readiness potential is electrical activity in the frontal lobes that indicates the initiation of a movement. The surprising results that Libet reported were that the readiness potential, brain activity to start a movement, starts first. Sometime later, the subject reports the conscious decision to move. A bit later, the subject reports that he has moved. Then a bit later still, the wrist flexor muscles start to contract. The

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[114] Libet, B., Gleason, C.A., Wright, E.W. & Pearl, D.K. 1983. Time of conscious intention to act in relation to onset of cerebral activity (readiness potential) - the unconscious initiation of a freely voluntary act. *Brain* 106, 623-642.

order of events that Libet demonstrated shows that activity in the brain to start a movement precedes the conscious intent to move, and that the sensation that the movement has started occurs before the actual movement. Thus, our behavior, the actual movement that we make, is not immediately dictated by consciousness. Consciousness becomes informed and involved before the actual performance of the motion, but consciousness does not initiate the preparation for the action.

OK, if consciousness is not involved in directing movements, perhaps it has a more executive role in setting goals. However, an increasing body of work shows that goal setting occurs at an unconscious level also[115]. Recent research challenges the entire notion of conscious will[116]. Biologists and neuroscientists do not yet understand what the role of consciousness is, but they are in increasing agreement on what the role is not. It does not seem to be involved in goal setting or in the immediate direction of movements. So, let's continue to consider a few of the findings of Evolutionary Psychology.

Nausea and Vomiting of Pregnancy

Women in all cultures in the first trimester of pregnancy typically develop what used to be called morning sickness, or pregnancy sickness. They develop heightened odor and taste sensitivities to some food odors that make those odors and tastes aversive. For example, many women who relish coffee suddenly find in early pregnancy that the smell of coffee is

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[115] Custers, R. & Aarts, H. 2010. The unconscious will: how the pursuit of goals operates outside of conscious awareness. *Science* 329, 47-50.

[116] Wegner, D. M. 2002. The Illusion of Conscious Will. Massachusetts Institute of Technology Press, Cambridge, MA

repugnant. The aversion to some foods is so strong that some women react with feelings of nausea and often vomit. This abrupt behavioral shift in food habits, formerly interpreted as an illness, is now understood to be an evolved adaptation. The nausea and vomiting of pregnancy only occurs during the first trimester, when the embryo is in the developmental stage called organogenesis. The basic body plan and the organ systems are being assembled. A disruption during this phase of development usually has dire consequences. Disruption during organogenesis may result in the death of the embryo or in profound birth defects. Disruptions later in pregnancy, during the growth phase, after the body plan and organ systems are established, are less likely to cause serious problems.

The odors and tastes that women in the first trimester of pregnancy find aversive are typically those from plant parts that contain many secondary compounds. Secondary compounds are the chemical defenses of plants; they evolved to deter herbivores, and they have a variety of toxic effects. They may inhibit digestion, poison metabolic pathways, or act as neurotoxins. Many are disruptors of development.   Thus, human females evolved a behavioral switch that helps them to avoid eating plants that may contain chemicals that disrupt development of the embryo during the critical period when it is laying out its body plan[117].

Reproductive Cycles

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[117] Profet, M. 1995. Pregnancy Sickness. Using Your Body's Natural Defenses to Protect Your Baby-to-Be. Addison-Wesley Publishing, Reading, California.

Human females are unusual mammals in that they do not signal ovulation. In most mammals, the moment of ovulation, when eggs burst from the ovary and enter the top of the reproductive tract, is associated with an event called estrus. In estrus, a female mammal broadcasts visual, chemical and behavioral signals of her state, and she becomes behaviorally receptive to male courtship. At any time outside of estrus, the female does not tolerate male advances. For example, in monkeys and in other apes, estrus is accompanied by pronounced swelling of the bare red skin around the vulva. This is an obvious, impossible to miss signal of ovulation. Humans, in contrast, do not have estrus. Ovulation is concealed, even from the ovulating woman, and there is no clearly defined period of sexual receptivity. There is a slight peak in sexual activity and in behavior that could be called sexual solicitation in women around the time of ovulation, but it is only just detectable. In addition, women living in proximity to each other (group members ancestrally, college dorm inhabitants in the present), tend to synchronize their menstrual cycles[118]. Synchrony is achieved by subliminal chemical cues that are present in armpit odor[119].

Why should human females have evolved this specialized form of reproductive cycling? The best guess at present is that the specialization is an outcome of sexual conflict. It is a way to blunt the force of male infanticide. If ovulation is concealed and sexual receptivity is spread out across most of the menstrual cycle, then a male has very limited information on paternity, even if his mate has had EPC. Nothing like the infanticide clock that works for

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[118] McClintock, M. K. 1971. Menstrual synchrony and suppression. *Nature* 229, 244-255.

[119] Stern, K. & McClintock, M. K. 1998. Regulation of ovulation by human pheromones. *Nature* 392, 177-179.

male mice is available, because the male has no reliable cue to indicate when the female became pregnant. A child is born. The primary mate may be the father because he copulated repeatedly with the woman. However, another male or males may be the father because of EPC. There is no easy way for a male to know for certain that he is the father or for certain that he is not the father. Thus, the motivation for infanticide is diminished.

This explanation relies on male infanticide being a risk when the male has more certainty of paternity. Is this true? Do human males practice infanticide when there is certainty that they are not the father of an infant? The answer is yes. We do not know what the ancestral rates of infanticide were, but even in modern western society, where the force of the law operates powerfully, the pattern is very clear. When a young infant (0-2 years of age) is living in a household with the mother and a male who is not the father, the infant's risk of suffering some form of physical abuse from the male is much higher than the risk for a child living in a household with both biological parents, and the risk of being killed by the stepfather is greatly elevated. In Canada, a child 0-2 years of age that lives with the mother and a stepfather has a 6 in 10,000 chance of being killed by the male. This rate of killing is 70 times greater than the rate at which young children are killed by the biological father[120]. These killings of stepchildren seem to stem from moments of rage by the male. In 82% of instances in which a stepfather kills a cohabiting child under five years of age, the method is by beating, as opposed to shooting, suffocating, or other means. A biological parent that kills a child is much more likely to use a gun[121]. More recently, Daly and Wilson, who

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[120] Daly, M. & Wilson, M. 1988. Homicide. Aldine de Gruyter, New York.

[121] Daly M. & Wilson, M. I. 1994. Some differential attributes of lethal assaults on small children by stepfathers versus genetic fathers. *Ethology and Sociobiology* 15, 207-217.

reported the data on infanticides in Canada, summarized evidence to show that the greatly elevated risk of infanticide when a male who is not the biological father is living with a young child is not unique to Canada - it is a world wide phenomenon[122].

Polygyny

Infanticide, as I indicated in Chapter 11, is a characteristic of polygynous species. Were humans ancestrally polygynous? There is quite a bit of evidence that they were. First, our species shows sexual size dimorphism. Human males are larger and more muscular than females. Second, there are differences in temperament. Human males are much more prone to physical violence; across many cultures they commit 93 -100% of murders. These murders overwhelmingly are about two things. They are about social status striving among other males, and they are about sexual jealousy. Violence in both arenas contributes to mating success.

Third, human males are behaviorally focused on copulation and on maximizing the number of different women that they copulate with. Abundant evidence, summarized by Laura Betzig, shows that with the start of agriculture and the sudden possibility that powerful individuals could monopolize resources, vast asymmetries in male mating success occurred. In culture after culture, a social organization in which to top leader who

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[122] Daly, M. & Wilson, M. (2008). Is the "Cinderella effect" controversial? A case study of evolution-minded research and critiques thereof. Pp.381-398 in C.B. Crawford & D. Krebs, eds., Foundations of evolutionary psychology. Erlbaum, Mahwah NJ.

controlled a huge harem of females appeared[123]. Modern worldwide surveys indicate that in every culture, men state that they want many more (about 5 times more) sex partners than women do, and they indicate willingness to engage in sexual intercourse with an attractive woman almost immediately after meeting her. Women, in contrast, do not reach the male instantaneous willingness level until they have known a man for 3 to 6 months[124].

Fourth, human males have an adaptation to deal with sperm competition. This was revealed recently in a study of couples that agreed to report data on their copulations, to use a condom with each copulation, and to collect the condom contents in fixative immediately after each copulation. The hypothesis being tested was that males would alter the number of sperm ejaculated in relation to their perceived risk of sperm competition. The risk of sperm competition varies with the amount of time that a male can monitor his partner in between copulations. For example, suppose that Sally and Bill copulate on Monday morning. Then, Bill goes to a nearby city for a short conference. He comes home two days later, on Wednesday evening, and the couple copulates again that night. The interval between copulations was 65 hours, and the two partners were physically apart for 90% of that time. At the other extreme, suppose that Sally and Bill copulate on Monday morning. Then they spend the next two days painting their apartment, going out to dinner, and participating in their book club. They copulate again on Wednesday night. In this instance, the inter-copulation interval is again 65 hours, but the two partners have been apart none of the time.

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[123] Betzig, L. L.1986. Despotism and Differential Reproduction: A Darwinian View of History. Aldine, Hawthorne, NY.

[124] Buss, D. M. & Schmitt, D. P. 1993. Sexual strategies theory: an evolutionary perspective on human mating. *Psychological Review* 100, 204-232.

In the first example, Bill experiences a perceived risk of sperm competition because he could not monitor his partner for 60 hours. In the second example, Bill perceives no risk of sperm competition because he was physically close to Sally for the entire inter-copulation interval. The results? In the second scenario, where the pair was not separated for any of the 65 hour inter-copulation interval, Bill ejaculates about 200 million sperm. In the other scenario, where the two have been physically apart for the same interval, Bill ejaculates about 600 million sperm. Couples in this study reported times spent apart between copulations that ranged from almost zero to almost 100%, and the number of sperm ejaculated rose predictably as the time spent apart increased[125]. The number of sperm ejaculated had nothing to do with ejaculate volume, and neither member of the couple could perceive the difference. The number of sperm ejaculated is not under conscious control. The male need not even suspect that his partner is having EPC. The adjustment with EPC risk is simply an automatic thing that males do, like sweating when body temperature is too high, or shivering when body temperature is too low.

Do human females, as these results suggest, routinely engage in EPC? This may seem like a silly question, because the topic has a major role in literature and in daytime television. However, obtaining information on the rates of EPC and the circumstances under which it occurs is a very difficult task. In face-to-face interviews, the subjects may not be truthful, and building up an adequate sample size is very time consuming. The best way to get the information would be to clandestinely observe women, but this would not be ethical, and it

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[125] Baker, R. R. & Bellis, M. A. 1995. Human Sperm Competition. Copulation, Masturbation and Infidelity. Chapman & Hall, London.

also would be time consuming and labor-intensive. Baker and Bellis decided to try anonymous questionnaires. They arranged to publish the questionnaire in *Company* magazine in March-April 1989. The publisher estimated that the female readership of that issue was 439,000, or 5% of the UK population of reproductive age females. Baker and Bellis obtained 3,679 replies. This sample is the best information to date on the true nature of EPC by human females. The data show that as the level of sexual experience (defined by the number of lifetime copulations as of the date that the respondent filled out the questionnaire) increased, the percentage of females that reported a double mating (mating with two different males within 1 hour to 1 day) rose to about 70%. Almost no females reported being strictly monogamous, and the likelihood of EPC rose as the average time that the male partner was with the female declined. In other words, male mate guarding is needed to prevent EPC.

The principal value of Evolutionary Psychology is that it has the potential to revel our true natures. When everyone acknowledges the truth about human nature, then social institutions may relax a bit to be less dissonant with who we are. For example, in most modern cultures, there is a legal enforcement of monogamy. Evolutionary Psychology shows us that strict monogamy is definitely not the natural human mating system. Because of the extensive parental care that human infants require, humans may be more like songbirds. It seems that humans are socially, but not genetically monogamous.

War

There are only two mammal species in which males form cooperative coalitions to defend territory boundaries, kill territorial neighbors, and opportunistically abduct territorial neighbor females for sex. Those two species are chimpanzees and humans. Territorial war occurs in all the modern hunter-gatherer societies that anthropologists have found, and in technological societies it occurs in the context of urban gangs. War is unusual and it is rare among animals because it is a cooperative activity. As I noted in Chapter Nine, there are many circumstances that work against the evolution of cooperation, and especially against cooperation in which participants risk death. Thus, war may be limited to Chimpanzees and Humans because these two large-brained species have enough social intelligence to allow individuals to monitor many group members simultaneously, to check for signs of cheating. Even when the detection of cheaters is perfect, the only benefit of war that could outweigh the cost (risk of death) is increased mating activity. An increased number of wives or mates seems to be the rule for acknowledged warriors in preindustrial societies. Where long term data are available, the evidence shows that acknowledged warriors have enhanced fitness. They have greater numbers of surviving offspring than non-warriors[126]. In addition, one of the ubiquitous male activities in war is rape - a lot of rape. This is a phenomenon known from antiquity to the present.

Human males have brain reward mechanisms that result in group cohesion and effective coalition formation for war. Consider this passage, written by a combat Marine veteran who fought in the Vietnam War. A U. S. Platoon is starting to advance toward a fortified hilltop held by the NVA:

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[126] Chagnon, N. A. 1988. Life histories, blood revenge, and warfare in a tribal population. *Science* 239, 895-892.

> “Mellas, watching First Platoon’s backs, kept asking in a whisper, ‘Why? Why? Why?’ At the same time, immense excitement gripped him. He turned to Fitch. ‘You don’t need me here. I’m going with First Platoon.’ And not knowing why himself, he ran to catch up with the slowly moving platoon.
>
> Running to rejoin them, he felt overwhelming joy. It was as if he were coming home from a lashing winter storm to the warmth of his living room. The sky seemed brilliantly blue and clear, although he know it was overcast. If he didn’t move his legs faster, his heart would outpace his feet and burst. His heart, his whole body, was overflowing with an emotion that he could only describe as love.”[127]

Human males have evolved psychological mechanisms that result in effective temporary bonding and cooperative acts during war. Modern state warfare can exist because military training and organization is structured to create the social settings in which this behavioral switch is turned on.

Us versus Them

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[127] Marlantes, K. 2010. Matterhorn. A Novel of the Vietnam War. Atlantic Monthly Press, New York.

Because humans evolved in tribal, kin-centered, territorial societies, they also evolved a predilection to make discriminations between people that were members of the tribe (us) and people that were not members of the tribe (them). The formation of this discrimination also comes with emotional tags. Being surrounded by tribal members and especially engaging in coordinated activity with tribal members, is inherently rewarding, and exposure to non-tribal members evokes anger and fear. The urge to draw us/them distinctions in humans is universal and powerful, and it is trivially easy to turn on, and to exploit. It is the basis for racism. It is the basis for the ethnic hatreds that fester all over the world. It is the basis for the participation in team sports and the basis for intense fan identification with sports teams. It is the basis for organized religion, which draws its principal power from the separation of us from them (heathens, infidels) and from the performance of group ceremonies that excite the reward circuits for group coordinated activity. It is the basis for clubs, social organizations such as unions, and for political parties. Religion and politics are two topics to avoid in polite conversation because both rest upon us/them tribal identity, which is inflexible and unmodifiable. Finally, the us/them discrimination is what allows modern nation states to exist. That fact that political leaders of entire countries can evoke nationalistic sentiment is testimony to the ease with which the us/them switch is thrown in humans.

Here is another possible contribution that Evolutionary Psychology could make. If school children were taught about human evolutionary history and the existence of the us/them switch, they might emerge as adults that are a bit more tolerant, and a bit less likely to be led around by the nose by religious and political rhetoric. Rates of violence in modern technological societies are lower than rates in preindustrial societies. The past 60 years in the United States have proven that even virulent forms of racism can be overcome. Our ability to stay on this path will rest in large part on our willingness to explicitly recognize the reality of the us/them switch, to acknowledge that it is an evolved human trait that we cannot get rid of, and to move toward uses of the switch, such as organized sports, that are relatively benign. The us/them switch is the principal source of enmity among people. It should be acknowledged for what it is, and taken out of the hands of those who would wield it for money and power.

The worst consequence of the us/them switch is that it is the basis for genocide. Genocides are depressingly common. They are recorded from antiquity to the present, and they always start with an us/them discrimination. However, although the us/them discrimination is necessary for genocide to occur, it does not seem to be sufficient. There are plenty of choleric racial, ethnic and religious hatreds going on at any time, and most never become genocide. There are likely other behavioral switches that are required to move men to the point at which they are willing to hack many other people to death with a machete, but at present, we do not know precisely what those switches are. This is a job for Evolutionary Psychology. We need to identify the antecedent conditions in human evolution that promoted the emergence of the ability to engage in mass killing. If we could identify certain key stimuli that must be present for us/them to be converted into genocide, then we could possibly prevent genocides. Then again, it may turn out that no such switch can be found. It may be that only the us/them discrimination, followed by the right opportunity, is required. Currently, chimpanzees do not commit mass killings of other chimp groups. They go on organized patrols, in which they probe the defenses of a neighboring territory, and kill the occasional victim when then find him alone. But this may be simply because they lack technology.

Performance

The PET scan device is a way to look at ongoing brain activity. When a neuron is active, sending and receiving hundreds of action potential per second, it runs its sodium-potassium pumps as fast as possible and it consumes a lot of energy. Active neurons thus require the transport services of blood to deliver oxygen and glucose, and to carry away carbon dioxide. PET scans indicate where neurons are active by showing differences in local blood flow across the brain. In a recent study, researchers recorded PET scan brain activity while the subject, reclined on her back with her head in the PET scanner, moved her feet on an angled platform to perform tango steps to music. Even in this easy form of recumbent dancing, the researchers detected over twenty discrete areas, widely distributed in the brain, that were involved in producing steps that were entrained to a music[128]. This PET scan study conformed what most of already know. Dance is a skilled, difficult activity. A dancer performing a challenging choreography reveals the absolute limits of human motor performance.

Dance occurs in all human cultures, usually in conjunction with music, which provides a rhythmic beat to which dance movements are entrained. Although dance often has

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[128] Brown, S., Martinez, M. J. & Parsons, L. M. 2005. The neural basis of human dance. *Cerebral Cortex* 16, 1157-1167.

ostensible meaning for specific religious, or symbolic aspects of culture, it also has at least two deeper functions. First, it is commonly a coordinated group activity. Participation in coordinated group activities is inherently rewarding (often intensely rewarding) for humans. For humans, brain punishment and reward circuits define being alone as bad and define being harmoniously in a group as good. Dancing may thus qualify as a genuinely cooperative activity, in which performers mutually agree to an activity that promotes group solidarity.

The other function of dancing is sexual display. Dancing is another way in which males compete for mating opportunities and in which females can evaluate the possible genetic value of males. Many ethnographic studies have reported that dance functions in courtship, and many have noted that females seem to evaluate male dances based upon the endurance and vigor of the dancer[129]. Modern laboratory studies are arriving at the same conclusion. For example, female evaluation of male dance quality is correlated with independent measures of male physical strength[130].

The Dogon are a relatively isolated group of people who have lived along a sandstone escarpment in Mali, about 250 km south of Timbuktu, for the past several hundred years. They have developed a fascinating cultural institution called masked dancing. Only males dance. Individuals wear masks, but these are only part of the costume. The dancer's entire

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[129] Hugill, N., Fink, B., & Neave, N. 2010. The role of human body movements in mate selection. *Evolutionary Psychology* 8, 66-89.

[130] Hugill, N, Fink, B., Neave, N. & Seydel, H. 2009. Men's physical strength is associated with women's perceptions of their dancing ability. *Personality and Individual Differences* 47, 527-530.

dress and his postures and movements transform him into a mask. Some of the masks are quite difficult to manage:

> "Then the other masks get their share of attention. The spectacular tiu, four to five meters high, move in together like a walking thicket of trees. Like all wooden headpieces, this huge one, representing both a tree and a clan house, not only rests on the dancer's head but is tied to his waist with strips of cloth through a mesh of cords at the back. To maneuver, the dancer bites on a grip inside the headpiece. It takes good teeth as well as a strong neck to dance this mask, as the huge contraption has to move vigorously. Swaying the tree to and fro, each time touching the ground, and whirling it around horizontally, the dancer shows himself a real *sagatara,* a strong young man, eliciting shouts of praise from the bystanders, who keep at a safe distance (fig. 8). One of the performers fails in raising his mask from the ground and is booed away, while the spectators chatter about who he is, and why he lacks strength." [131]

Beverly Strassmann, who has studied many aspects of the ecology and reproductive lives of these people, notes that these tall masks are also dangerous. They could break the neck of an unskilled dancer. Strassmann writes that another mask, the stilt-walker, in which the dancer's legs are lashed to tall sticks, is even more dangerous. Although the dancers are

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[131] Van Beek, W. E. A. 1991. Enter the Bush. A Dogon Mask Festival. https://openaccess.leidenuniv.nl/handle/1887/9027

formally considered to be anonymous, Strassmann notes that female observers can identify individuals, and she writes that women watch dances "intently."[132]

I have presented just a few of the findings from Evolutionary Psychology. the examples I chose are those that to me seem firmly rooted in biology and in which the evidence is compelling. Evolutionary psychologists have taken up many other issues, and often the methods and standards of evidence are weak. This has led some to caricature the field as just so much story telling. I am afraid that I agree in part, but I would like to see Evolutionary Psychology persist. As I have suggested, this line of research has the potential to give us new insights about ourselves. In some instances, the information can have practical utility.

Evolutionary Psychology is a strange discipline, in that the premise, that fundamental human behavior should reflect adaptation to a stone age, tribal, territorial life, seems unassailable, but that the actual tests of hypotheses often are weak, indirect, and open to ridicule. Nevertheless, I hope that those who bravely work in this new field will soldier on, and that the well established facts from Evolutionary Psychology will be introduced into public school curricula. The most famous of the inscriptions carved into the wall of the Temple of Apollo at Delphi is "know thyself."

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[132] Strassmann, B. I. 2003. Social monogamy in a human society: marriage and reproductive success among the Dogon. pp 177- 189 in *Monogamy. Mating Strategies and Partnerships in Birds, Humans and Other Mammals* (U. H. Reichard & C. Boesch, eds.). Cambridge University Press, Cambridge.