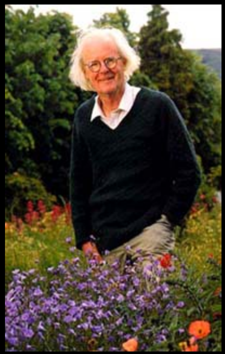
Conflict and Aggression

Conflict and Aggression

- Animals (like humans) have conflicts all the time.
- These need not involve physical aggression.
- What are the rules?

Game Theory: Model = Rules of Animal Conflict

- ***Optimality models*** usually consider animal's fit to the environment independent of other animals.
- ***Game theory*** predicts fitness optimization based on other individuals.
- The initial motivation was to explain why animals did not fight to the death.



Prisoner's Dilemma

	Cooperate	Defect
Cooperate	Reward You both keep quiet You both get -2 years	Sucker You keep quiet Partner gives you up You get -10 years
Defect	Temptation You defect give up your partner Your partner is quiet You get out free 0	Punishment You both give up the other. And both get Charged major crime You both get -8 years

T>R>P>S
(T+S)/2<R

-2 years for the minor crime
-8 years for the major crime

http://bio150.chass.utoronto.ca/pdgame/index.html

W.D. Hamilton

The Evolution of Cooperation

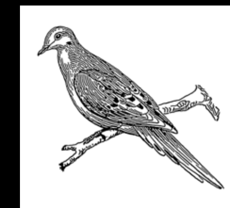
Robert Axelrod; William D. Hamilton

Science, New Series, Vol. 211, No. 4489. (Mar. 27, 1981)

Robert Axelrod

Game Theory: Building the Model

- *Step 1*: Specify tactics.
- *Step 2*: Specify payoffs.
- *Step 3*: Find the evolutionary stable strategy *(i.e. explain what we see)*



NATURE VOL. 246 NOVEMBER 2 1973

The Logic of Animal Conflict

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Conflicts between animals of the same species usually are of "limited war" type, not causing serious injury. This is often explained as due to group or species selection for behaviour benefiting the species rather than individuals. Game theory and computer simulation analyses show, however, that a "limited war" strategy benefits individual animals as well as the species.

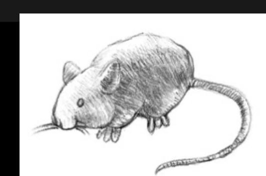
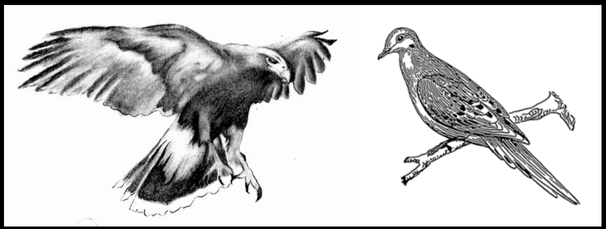


Table 1 Average Pay-offs in Simulated Intraspecific Contests for Five Different Strategies

		Opponent				
		"Mouse"	"Hawk"	"Bully"	"Retaliator"	"Prober-Retaliator"
Contestant receiving the pay-off	"Mouse"	29.0	19.5	19.5	29.0	17.2
	"Hawk"	80.0	−19.5	74.6	−18.1	−18.9
	"Bully"	80.0	4.9	41.5	11.9	11.2
	"Retaliator"	29.0	−22.3	57.1	29.0	23.1
	"Prober-Retaliator"	56.7	−20.1	59.4	26.9	21.9

Step 1: Specify alternative strategies/tactics

- Animals are phenotypically indistinguishable, but behave in a conflict in one of two ways (tactics).
- ***Hawk***: Always escalates and flees only if injured.
- ***Dove***: Display until an opponent gives up, flee if the opponent escalates.



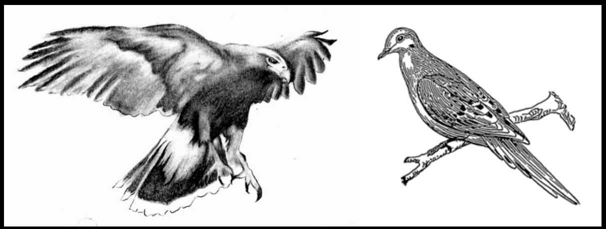
Step 2: Specify the payoffs

$p((V-C)/2) + (1-p)V = p(0) + (1-p)V/2$

$p = V/C$

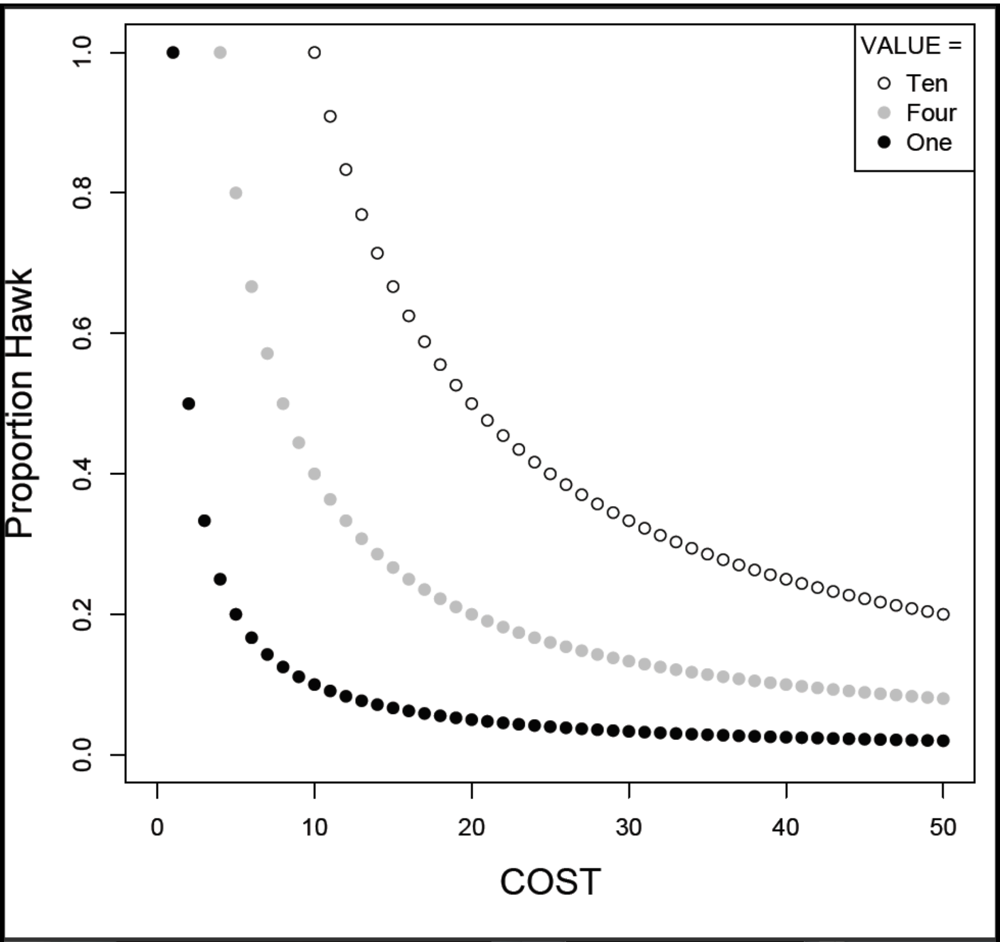
If V>C Hawk is an ESS but not Dove
If V<C neither pure hawk or pure dove is ESS

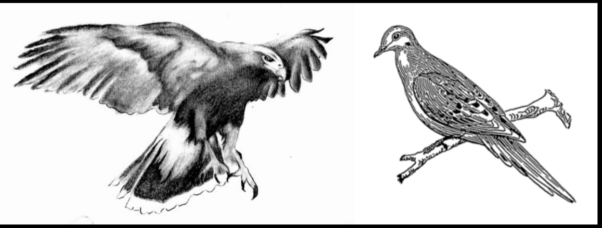
	Hawk (p)	Dove (1-p)
Hawk	(V-C)/2	V
Dove	0	V/2



$$p((V-C)/2) + (1-p)V = p(0) + (1-p)V/2$$

$$p = V/C$$





How are animals more complex than this model?

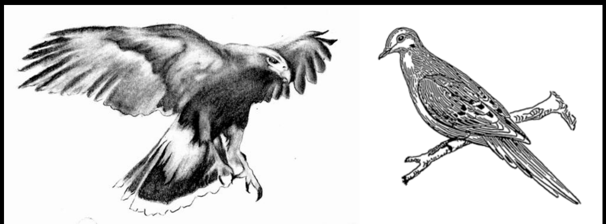
Step 2: Specify the payoffs

$p((V-C)/2) + (1-p)V = p(0) + (1-p)V/2$

$p = V/C$

If V>C Hawk is an ESS but not Dove
If V<C neither pure hawk or pure dove is ESS

	Hawk (p)	Dove (1-p)
Hawk	(V-C)/2	V
Dove	0	V/2 - toll **Add costs**



Step 2: Specify the payoffs

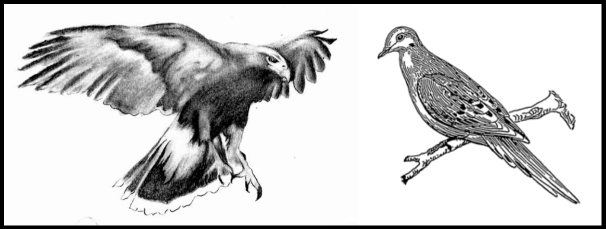
	Hawk (p)	Dove (1-p)
Hawk	**V/2-C**	**V**
Dove	0	V/2

Not all Ind. =

p((V-C)/2) + (1-p)V = p(0)+ (1-p)V/2

p = V/C

If V>C Hawk is an ESS but not Dove
If V<C neither pure hawk or pure dove is ESS



Step 2: Specify the payoffs

-p)

	H	D	R
H	$\frac{1}{2}(V - W)$	V	$\frac{1}{2}(V - W)$
D	0	$\frac{1}{2}V - T$	$\frac{1}{2}V - T$
R	$\frac{1}{2}(V - W)$	$\frac{1}{2}V - T$	$\frac{1}{2}V - T$

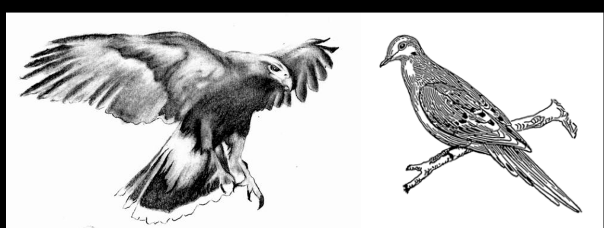
Dove 0 V/2

Additional tactics

p((V-C)/2) + (1-p)V = p(0)+ (1-p)V/2

p = V/C

If V>C Hawk is an ESS but not Dove
If V<C neither pure hawk or pure dove is ESS

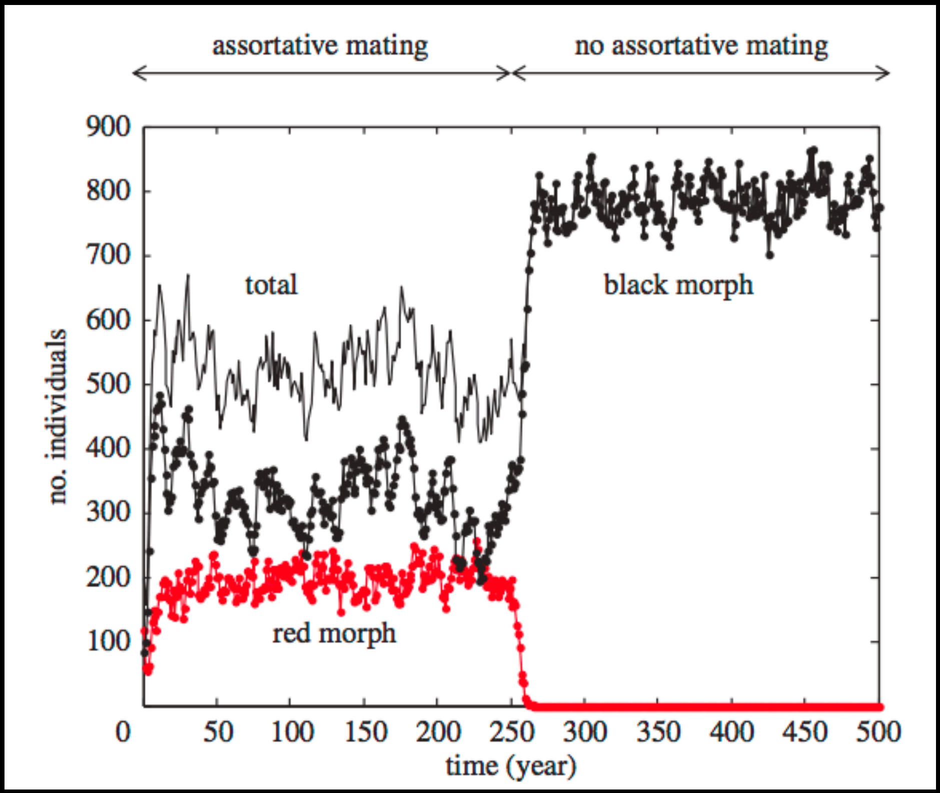


Red birds are more aggressive
(high testosterone)
Red birds have priority access to nest cavities
(a zero-sum game)
Red birds have fewer surviving offspring with red neighbors
(reduced parental effort)
Birds mate assortatively
(genetic incompatibility)

	Hawk (p)	Dove (1-p)
Hawk		
Dove		

Hanna Kokko
University of Zurich

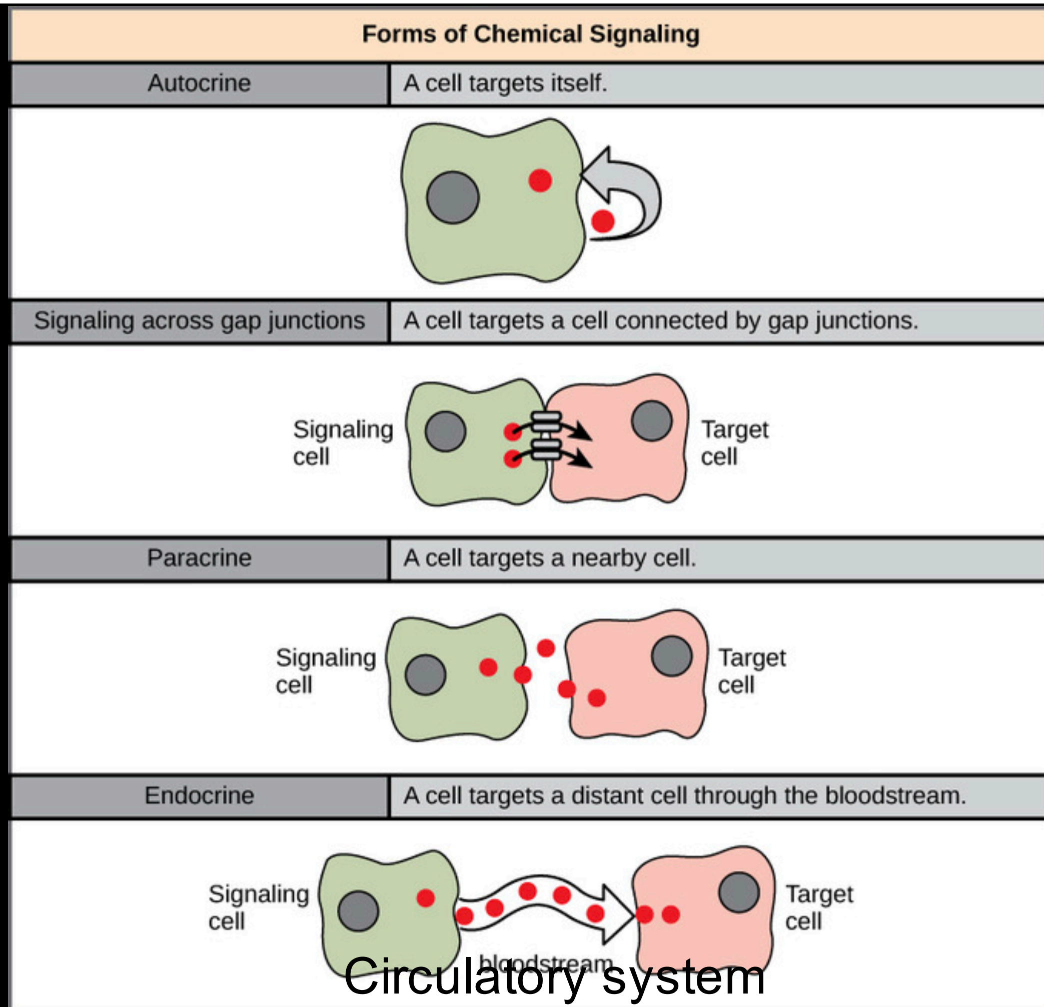
Kokko et al 2014 Proc. R. Soc. B 281: 20141794



Ecological model

Hanna Kokko
University of Zurich

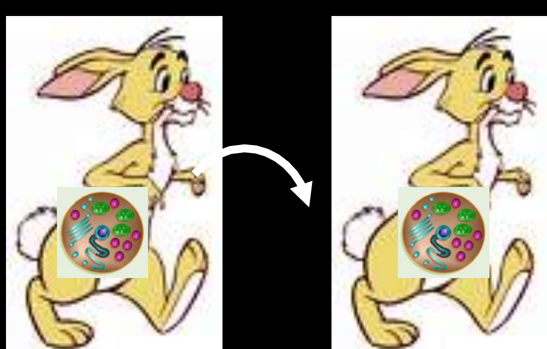
Kokko et al 2014 Proc. R. Soc. B 281: 20141794



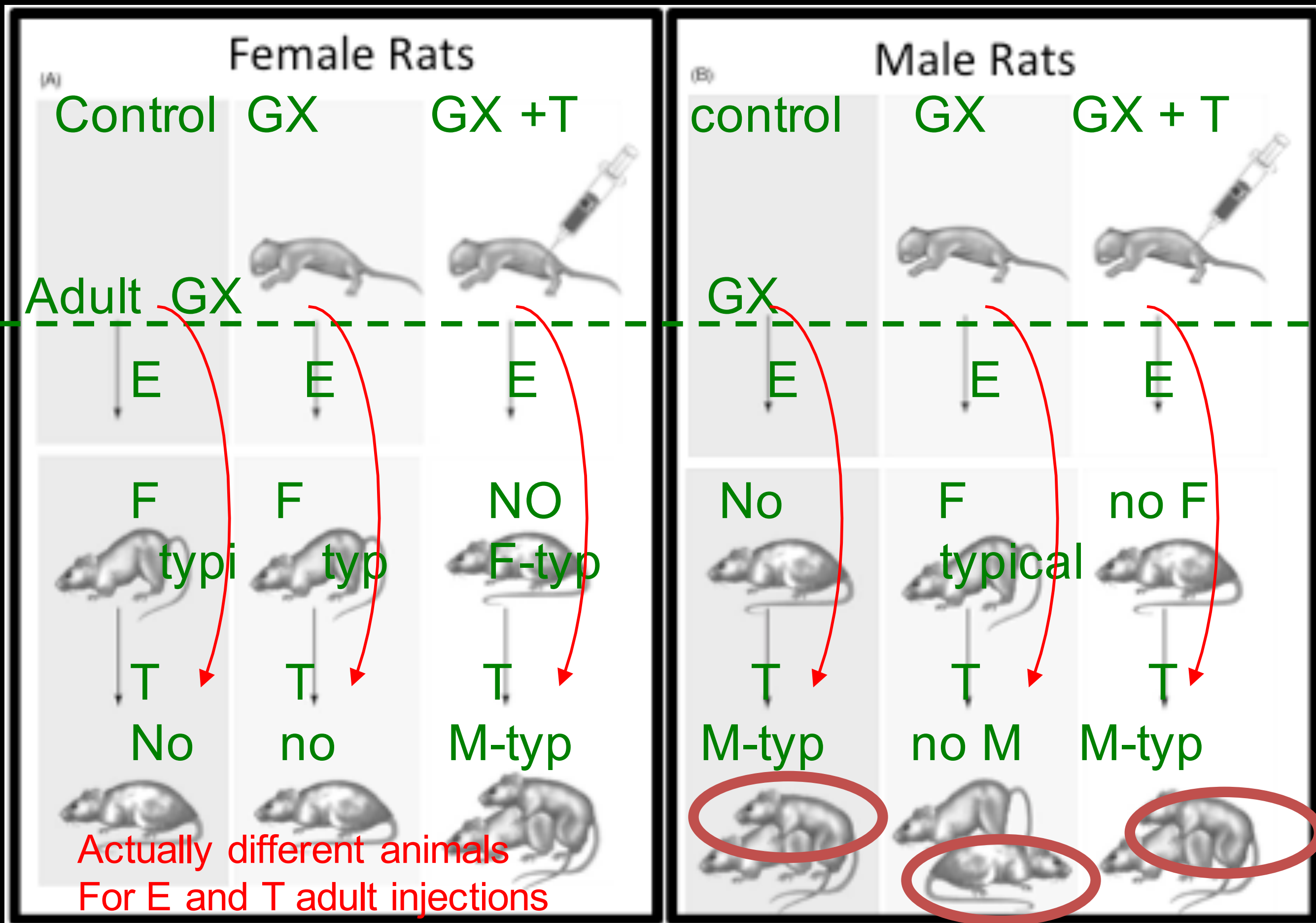
Autocrine

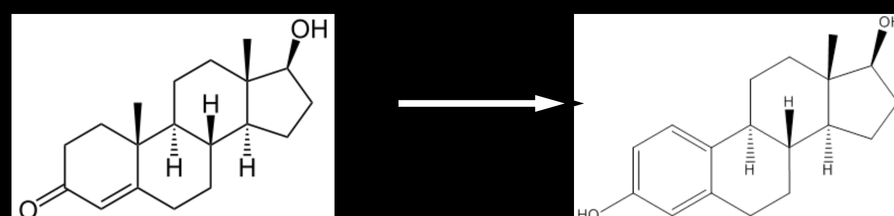
Paracrine

Endocrine



Exocrine (allocrine) – released/transferred SPECIFIC RECEPTORS RATHER THAN GENERAL SENSORY SYSTEM INTEGRATION WHICH IS BEST CONSIDERED COMMUNICATION

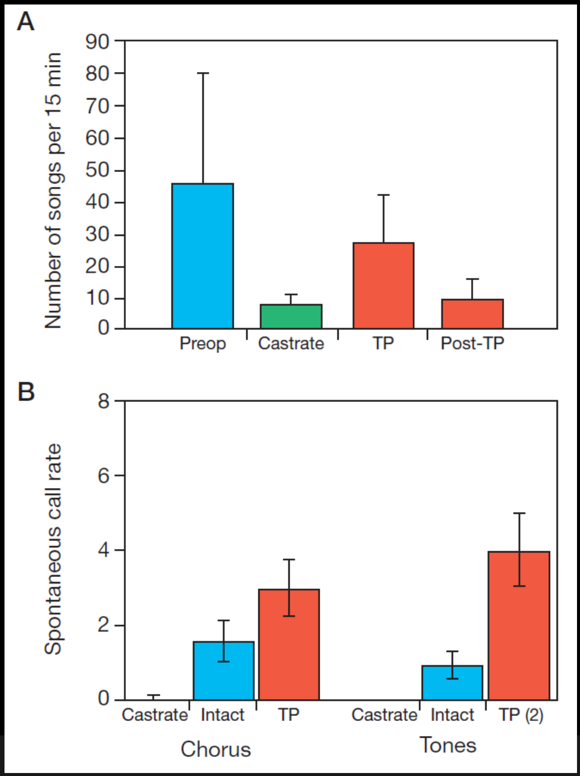




Testosterone

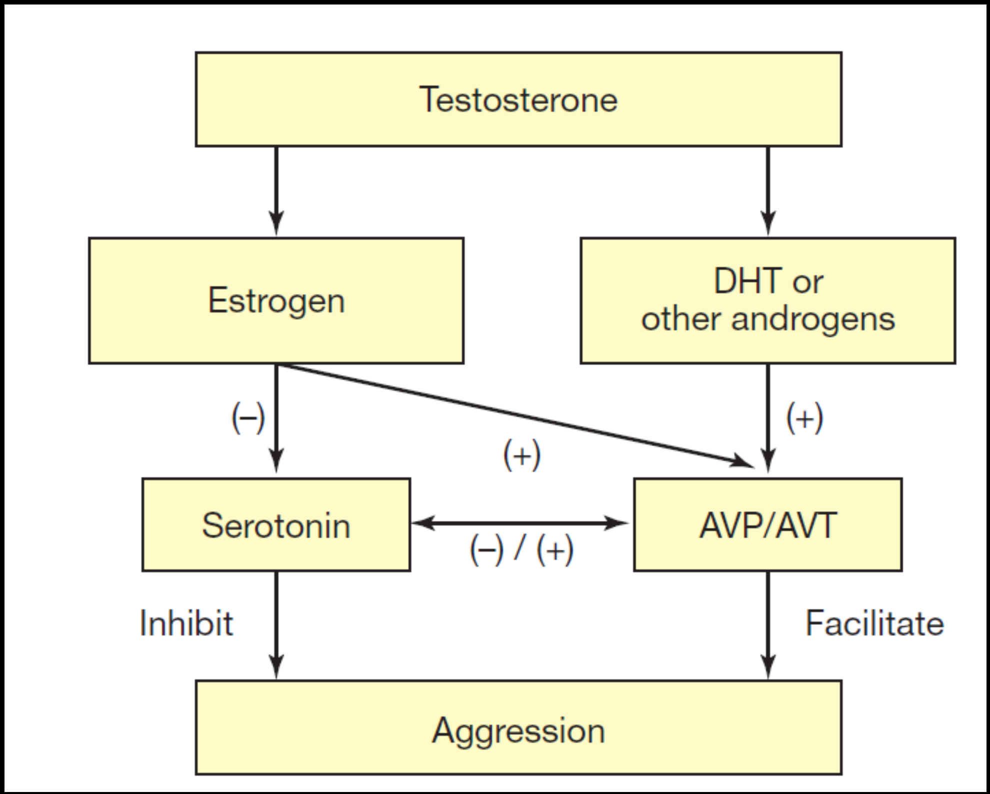
Estrogen

How do we know that T is important?



(A) Territorial singing in zebra finches drops after castration, is restored by implanting testosterone propionate (TP), and then drops again if the testosterone implant is removed.

(B) Similarly in frogs, spontaneous calling is absent in castrated males, compared to normal males, and testosterone implants raising levels above normal average results in high levels of calling. The effects are present whether or not frogs had previously been exposed to conspecific calls (Chorus) or to control random tones (Tones).



- T has important effects of two neuromodulators, serotonin and AVP/AVT.
- Infusing AVP into the anterior hypothalamus > aggression in hamsters only if T is present
- Serotonin reduces aggression.
- There are differences among species especially vert. versus inverts., e.g. serotonin > aggression in crabs

Do Isotocin and the Amygdala Mediate the "Dear Enemy" Effect?

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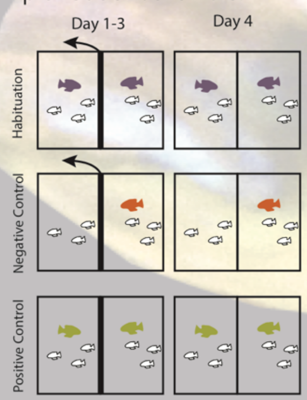
Introduction

Neighboring territorial males of many species exhibit less aggression toward each other than toward strangers, a phenomenon known as the "dear enemy" effect. While this effect occurs across taxa, the neuromolecular mechanisms remain unknown. The oxytocin (OT) pathway serves a critical role in mediating male-female pair bonding in several species and thus is an interesting candidate mediator of male-male bonding.

Model System: *Astatotilapia burtoni*

An established model system in social neuroscience, *A. burtoni* display extraordinary cognitive abilities in a social context dependent manner, making them an excellent system in which to investigate the neural bases of complex social behaviors.

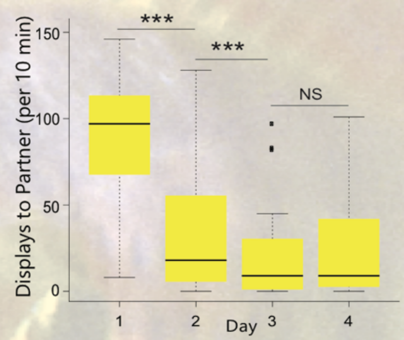


Hypothesis

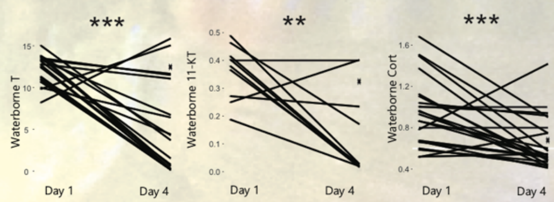
Isotocin (IT), the teleost homolog of OT, and its receptor (ITR) mediate habituation in aggression in the context of the "dear enemy" effect.

Territorial Neighbors Show "Dear Enemy" Effect

Repeated exposure to a familiar rival leads to reduced aggressive displays over time



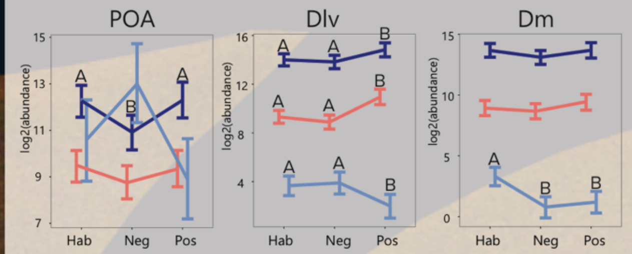
Social habituation is associated with reduced levels of androgens and cortisol



Candidate Brain Regions

POA: Neuroendocrine relay center, mediates aggressive behavior
Dm (put. amygdala homolog): Integration center involved in mediating emotional behavior
Dlv (put. hippocampus homolog): Involved in spatial behavior and learning and memory

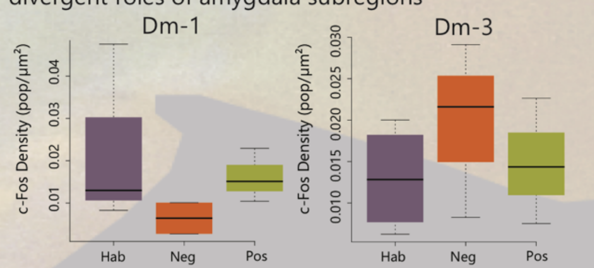
itr Responds to "Dear Enemy" Effect



c-fos: Immediate early gene, marker of neuronal activity
egr-1: Immediate early gene, marker of neuronal activity
itr: Nonapeptide, involved in social recognition and social motivation

"Dear Enemy" Effect is Reflected in Amygdala Activity

Preliminary immunohistochemistry data suggest divergent roles of amygdala subregions



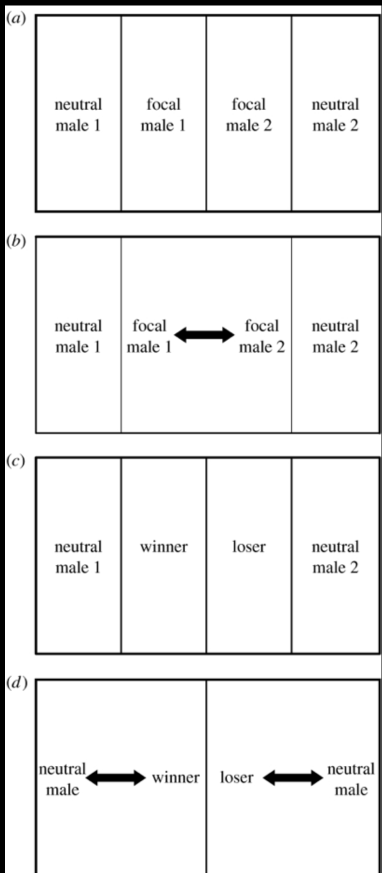
Ongoing Experiments

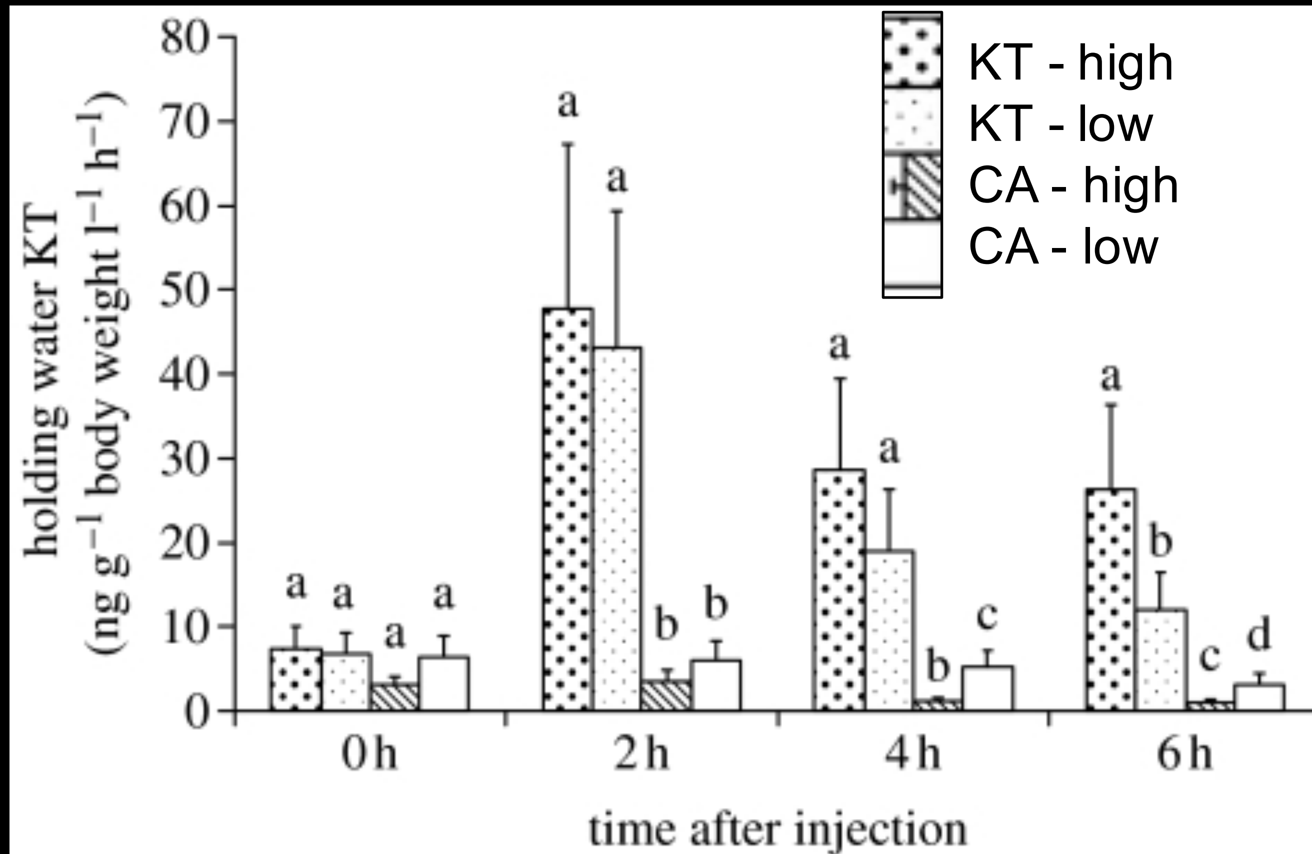
Double-labeling immunohistochemistry to identify the role of IT neurons activated in the "dear enemy" context.

Pharmacologically perturb the IT pathway to prevent the "dear enemy" effect.

Acknowledgements

We thank members of the Hofmann laboratory for discussion. This work was supported by NSF Graduate Research Fellowship to CAW, UT Undergraduate Research Fellowship to PD, NSF-IOS 1354942 to HAH.

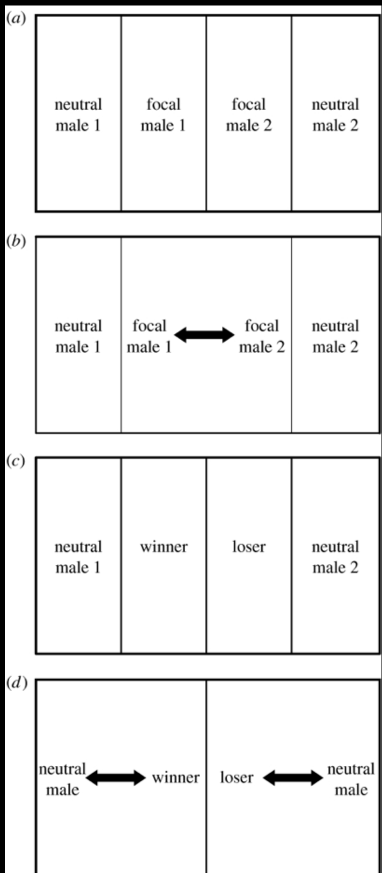


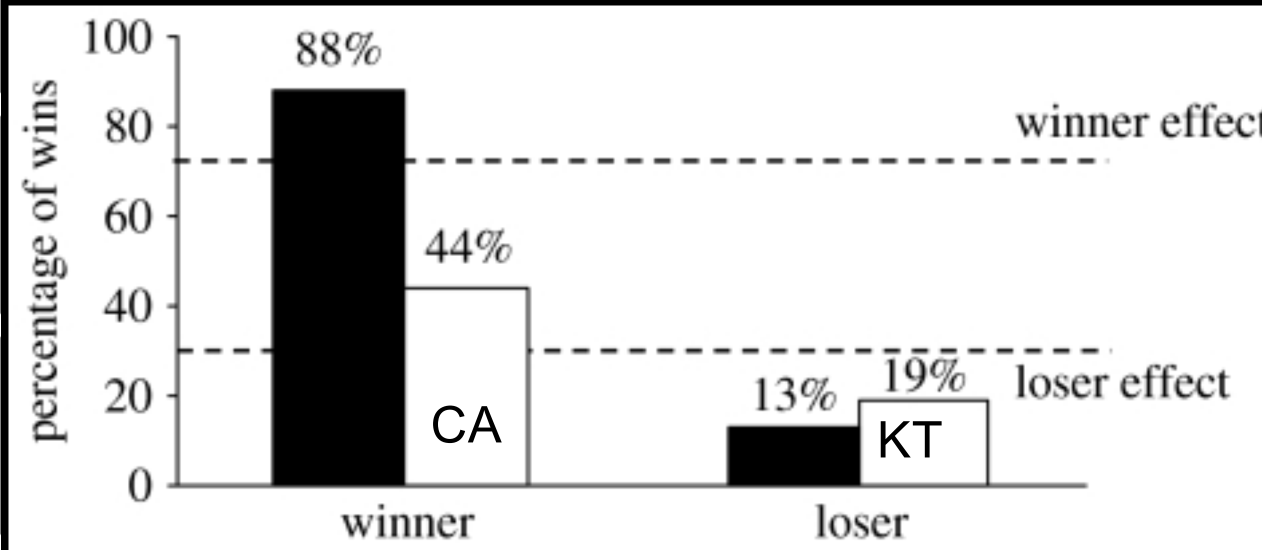



PROCEEDINGS OF THE ROYAL SOCIETY B
Proc. R. Soc. B (2009) **276**, 2249–2256
doi:10.1098/rspb.2009.0132
Published online 11 March 2009

Why do winners keep winning? Androgen mediation of winner but not loser effects in cichlid fish

Rui F. Oliveira[1,2,*], Ana Silva[1] and Adelino V. M. Canário[3]





0.67

0.33

Begin et al 1996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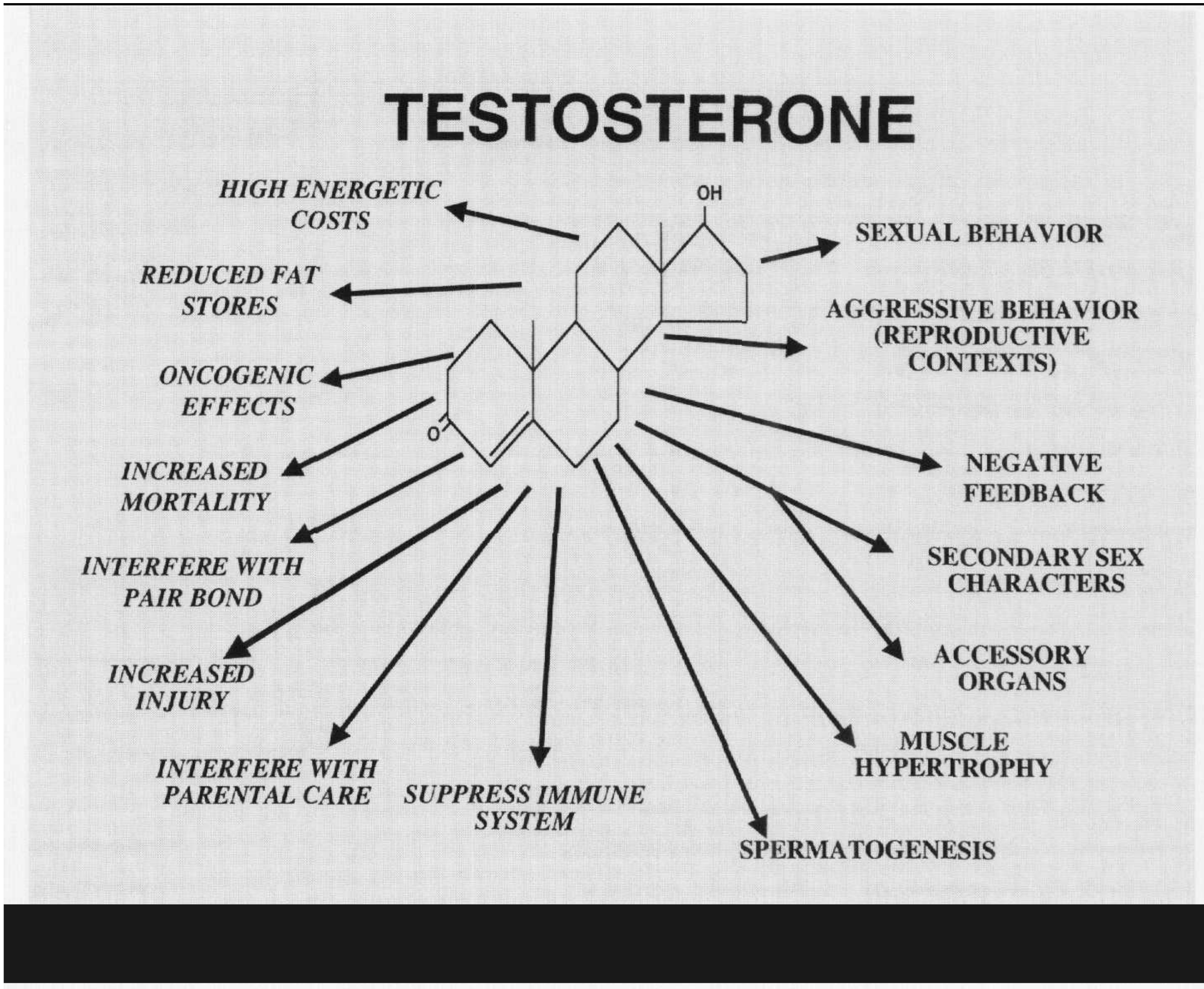
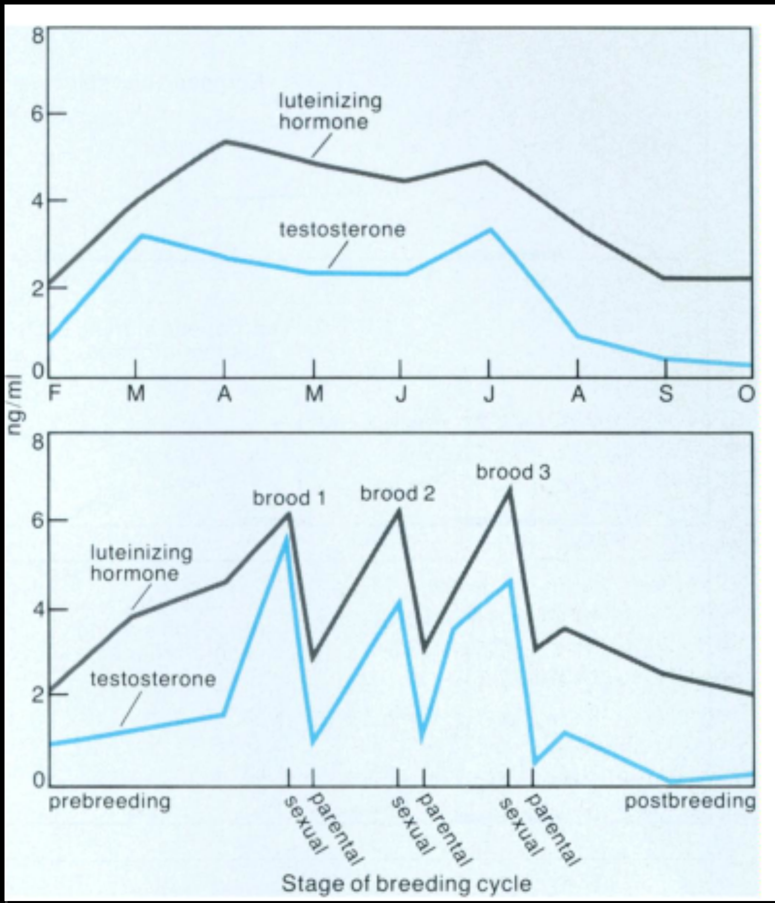

TESTOSTERONE
HIGH ENERGETIC COSTS
REDUCED FAT STORES
ONCOGENIC EFFECTS
INCREASED MORTALITY
INTERFERE WITH PAIR BOND
INCREASED INJURY
INTERFERE WITH PARENTAL CARE
SUPPRESS IMMUNE SYSTEM
SPERMATOGENESIS
MUSCLE HYPERTROPHY
ACCESSORY ORGANS
SECONDARY SEX CHARACTERS
NEGATIVE FEEDBACK
AGGRESSIVE BEHAVIOR (REPRODUCTIVE CONTEXTS)
SEXUAL BEHAVIOR
OH
O

How can an animal avoid the costs of Testosterone?

How can an animal avoid the costs of Testosterone?

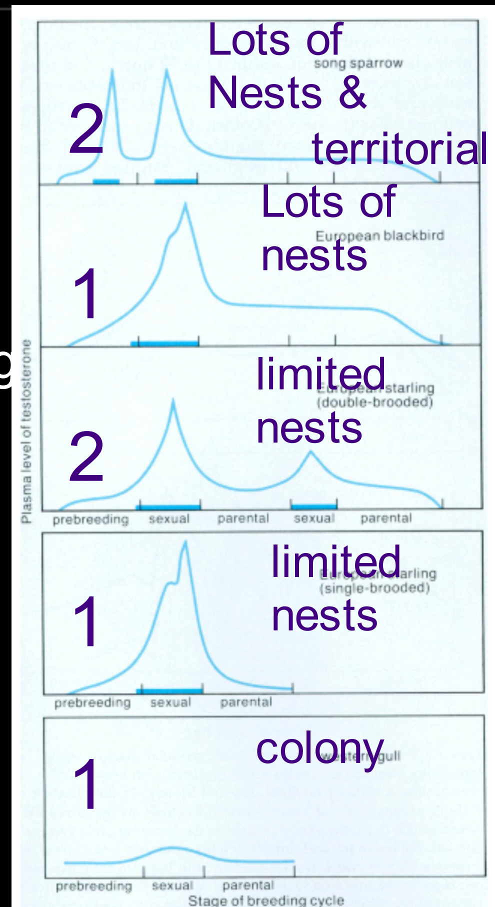
Resistance Hypothesis (just deal with it, or bind it and sequester it)
Social Modulation Hypothesis (make it when you need it)
Testosterone Insensitivity Hypothesis (most tissues have low receptor #)
Testosterone hypersensitivity Hypothesis (make tissues extra sensitive)
Circulating precursors (inactive until taken into cells)
Neurosteroid hypothesis (made in the brain)



New patterns emerge when hormone data are organized according to individual breeding cycle

2-peaks for song sparrow
1-establishing territory
2- egg laying

2-peaks for European Starling
1-1st brood
2- 2nd brood



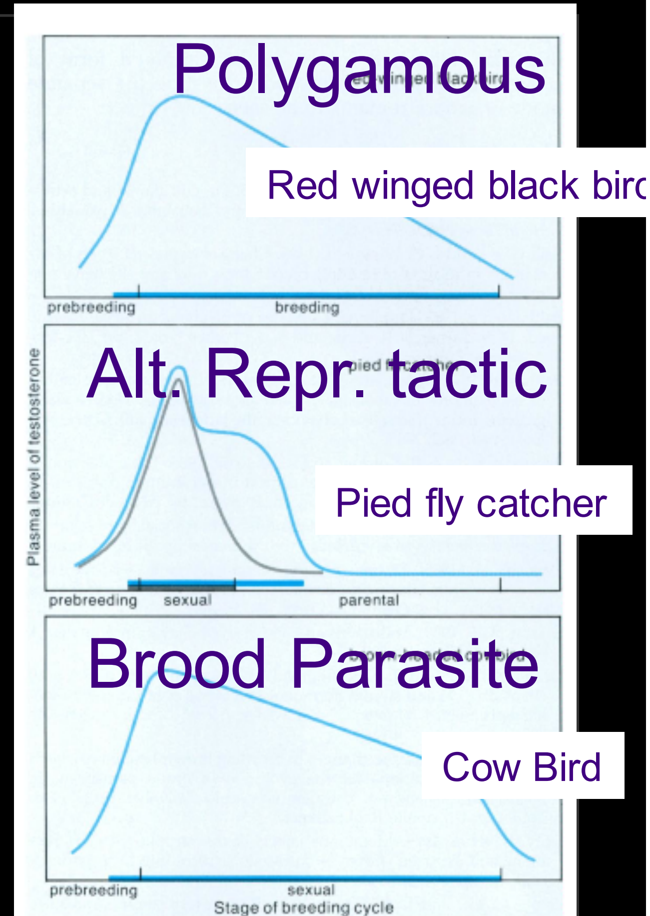
1-peak European black bird
only with egg laying
(plenty of open cup nests)

1-peaks for Western Gull
long lived pairs in colony

In Red-winged blackbirds, a polygynous or promiscuous species, males maintain high levels throughout competitive breeding season,

In some species, such as pied flycatcher, males show either polygynous or monogamous tactics and hormone levels differ such that monogoamous males show a shorter peak.

Brown cowbird males spend the season guarding females and competing with males. The females dump eggs in another “host” species nest.



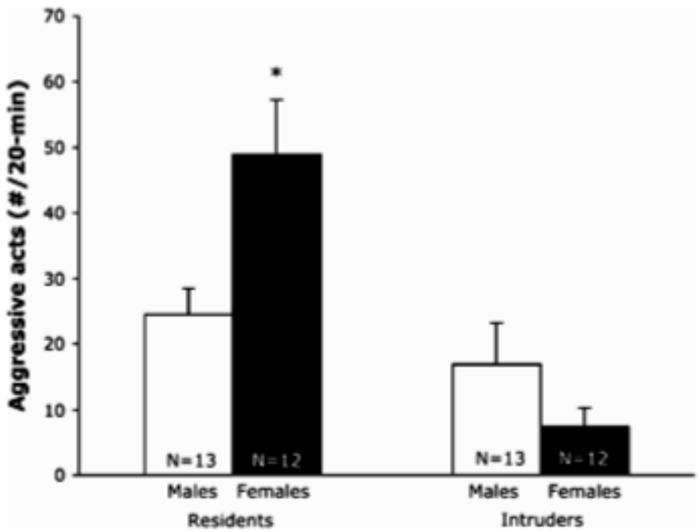
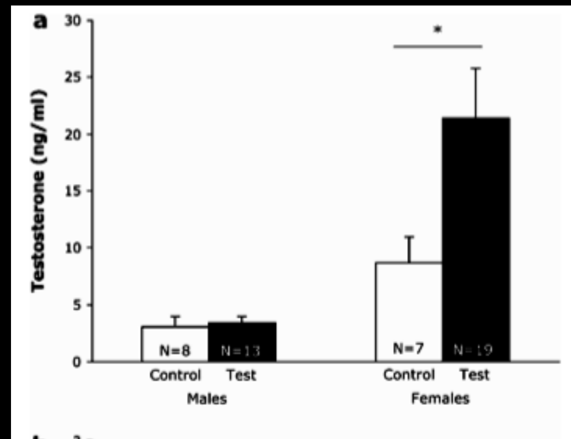
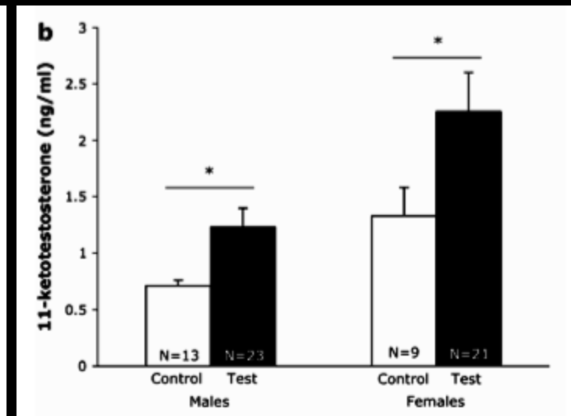
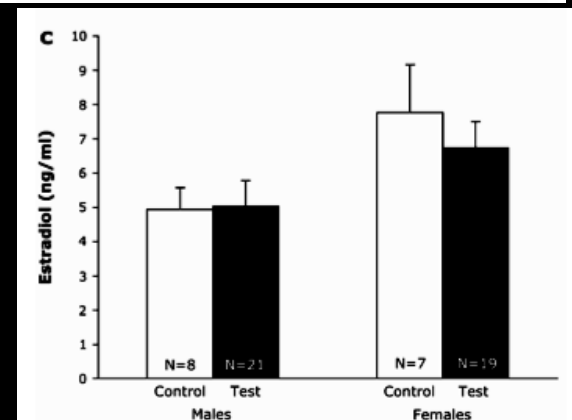


Figure 1
Mean (± standard error) number of aggressive acts displayed during a 20-min interaction of both male and female residents and intruders. The asterisk indicates a statistical difference at the $\alpha = 0.05$ level of a two-tailed paired t test.







Cichlid fish *Neolamprologus Pulcher*

Desjardins, J.K., Hazelden, M.R., Van der Kraak, G.J., Balshine, S. (2006) Male and female cooperatively breeding fish provide support for the “Challenge Hypothesis”. Behavioral Ecology 17:149

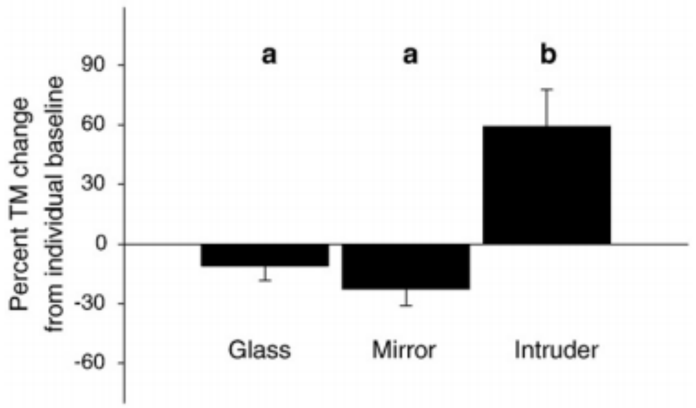
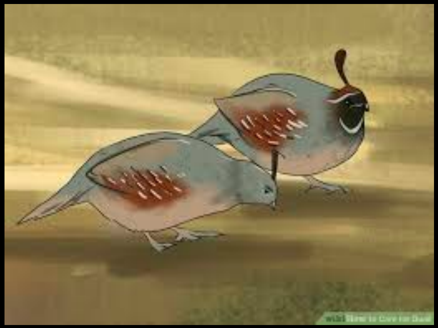


Fig. 3. Percent TM change of individual baseline TM levels in response to the different stimuli in male Japanese quail. Different letters indicate statistically significant differences between categories.



Social context rather than behavioral output or winning modulates post-conflict testosterone responses in Japanese quail (*Coturnix japonica*)

K. Hirschenhauser [a,*], M. Wittek [a], P. Johnston [a], E. Möstl [b]

Physiology & Behavior 95 (2008) 457–463

Pan troglodytes

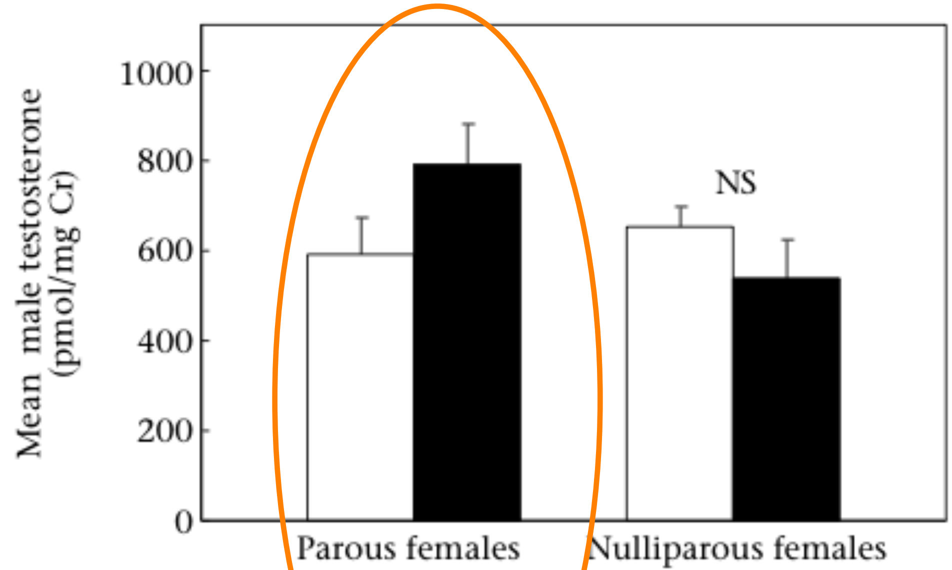
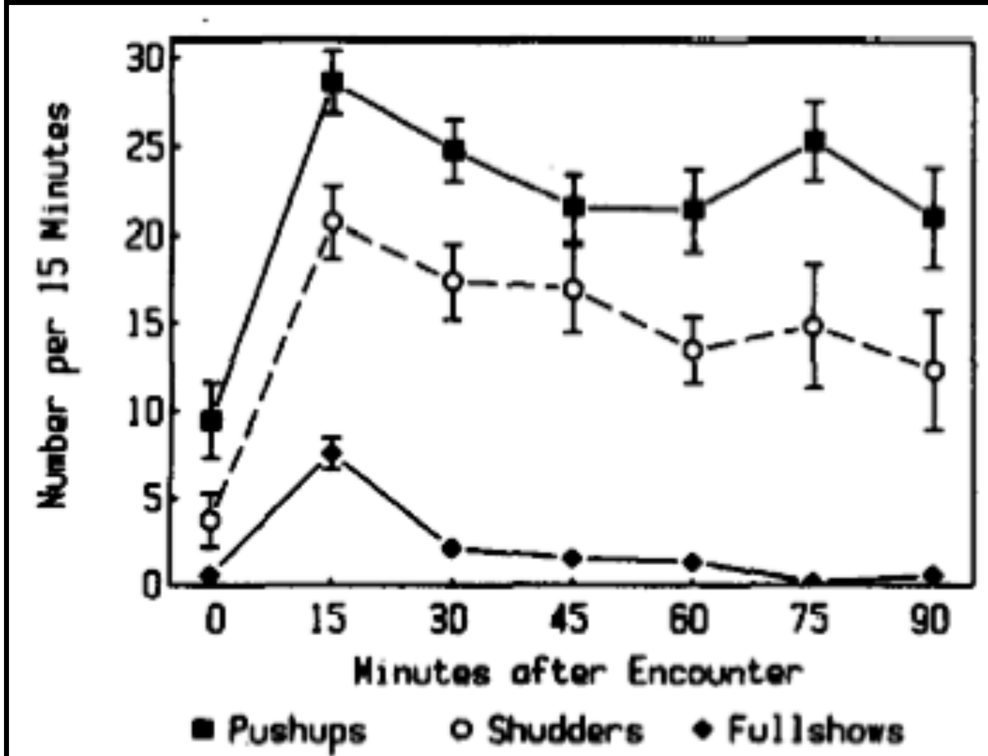


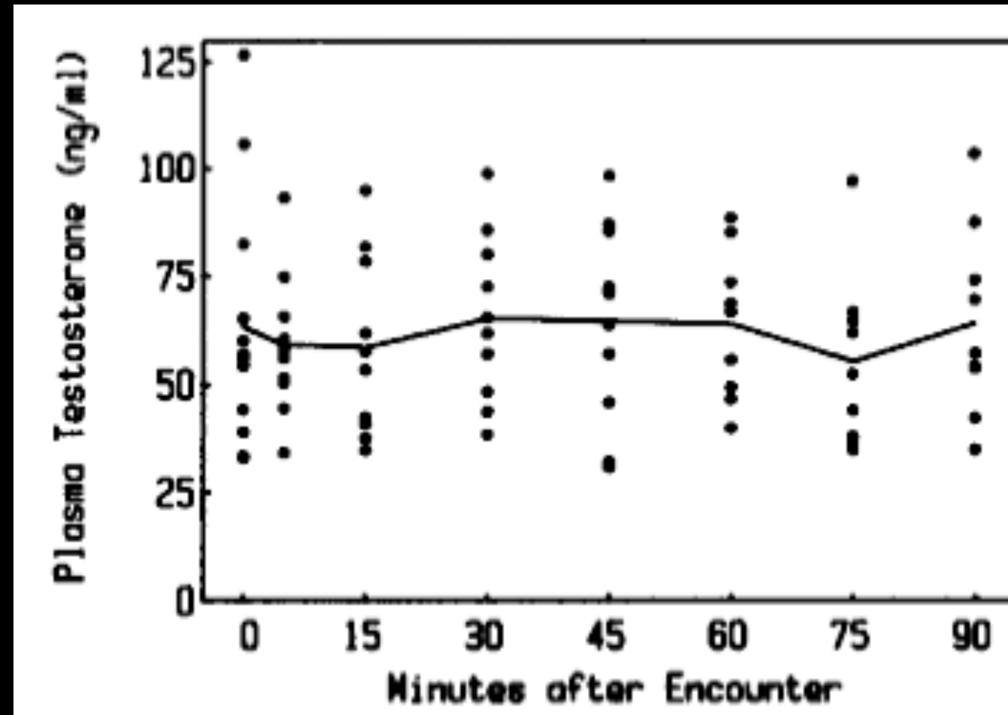
Figure 2. Male testosterone in mating (■) and nonmating (□) contexts.

Males fight over these females only

Males mate with all females

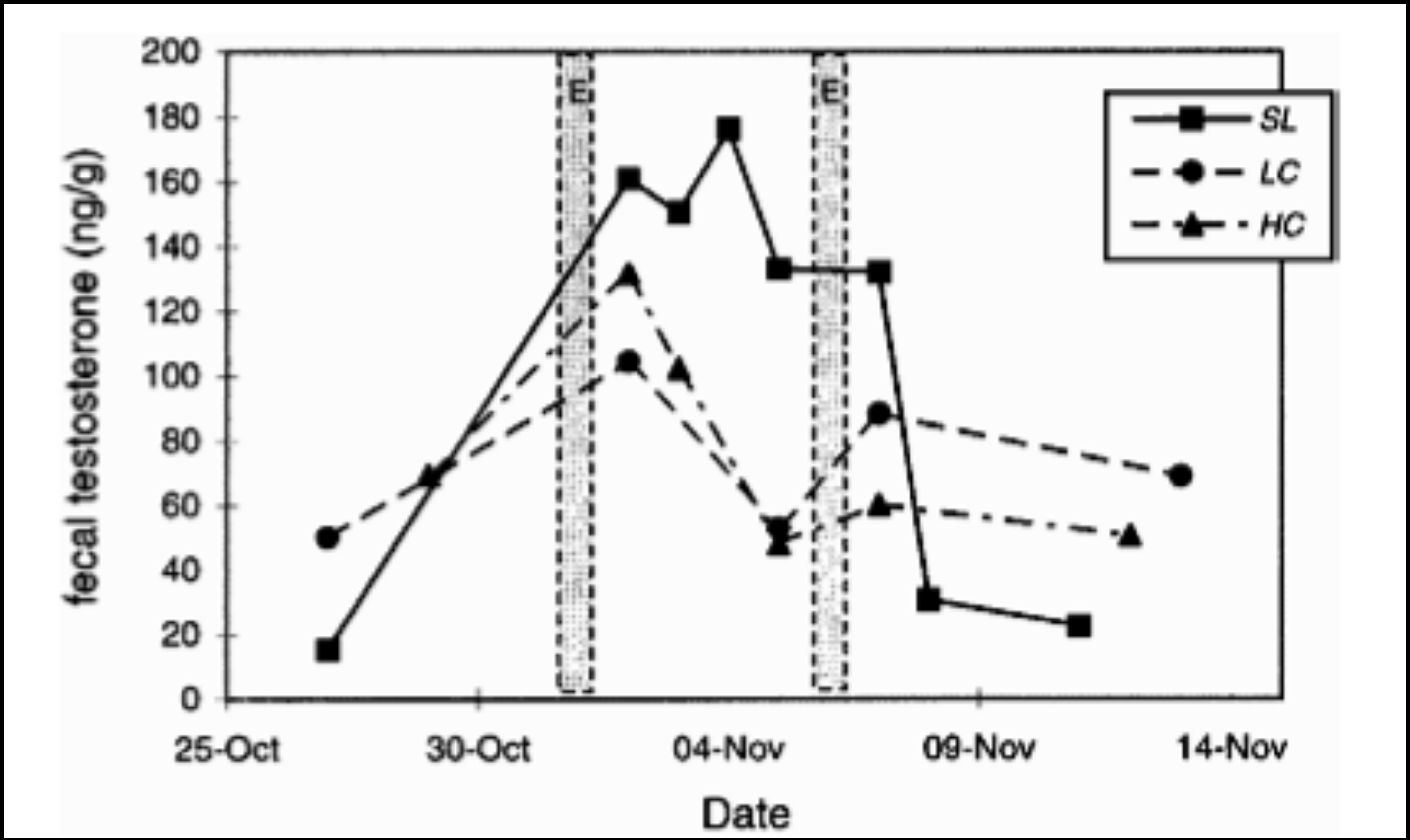
Muller, M.N., Wrangham, R.W., 2004. Dominance, aggression and testosterone in wild chimpanzees: a test of the challenge hypothesis. Anim. Behav. 67, 113-123.





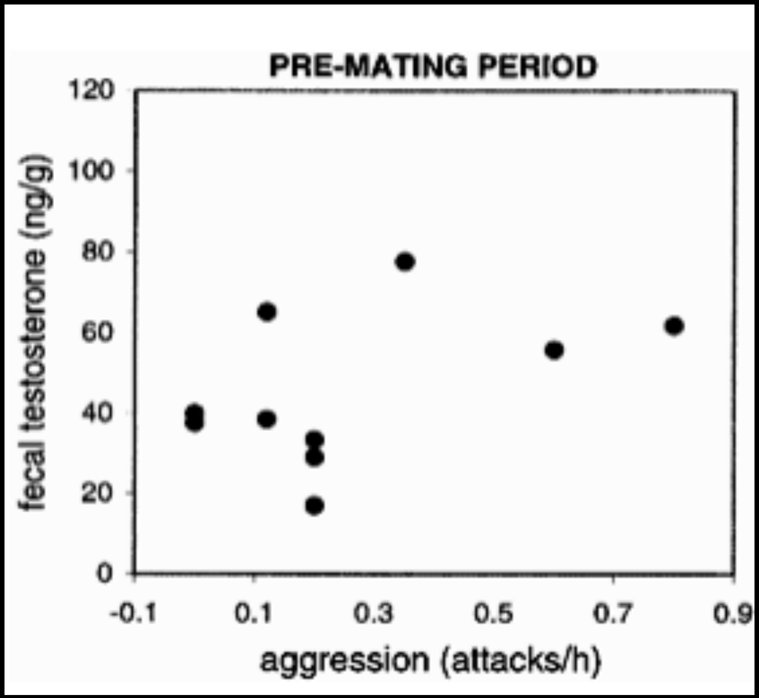
Sceloporus jarrovi

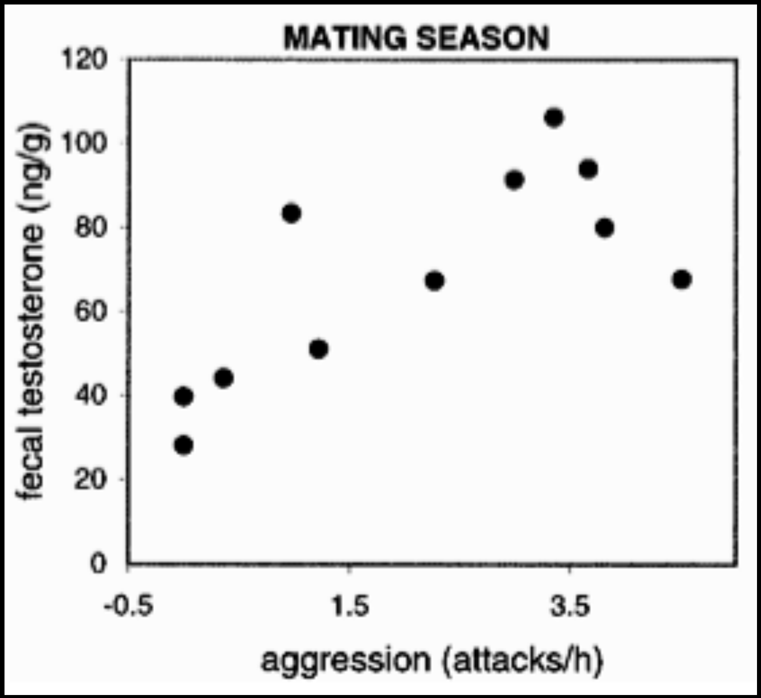
Moore, M.C., 1986. Circulating steroid hormones during rapid aggressive responses of territorial male mountain spiny lizards, *Sceloporus jarrovi.* Horm. Behav. 21, 511–521.



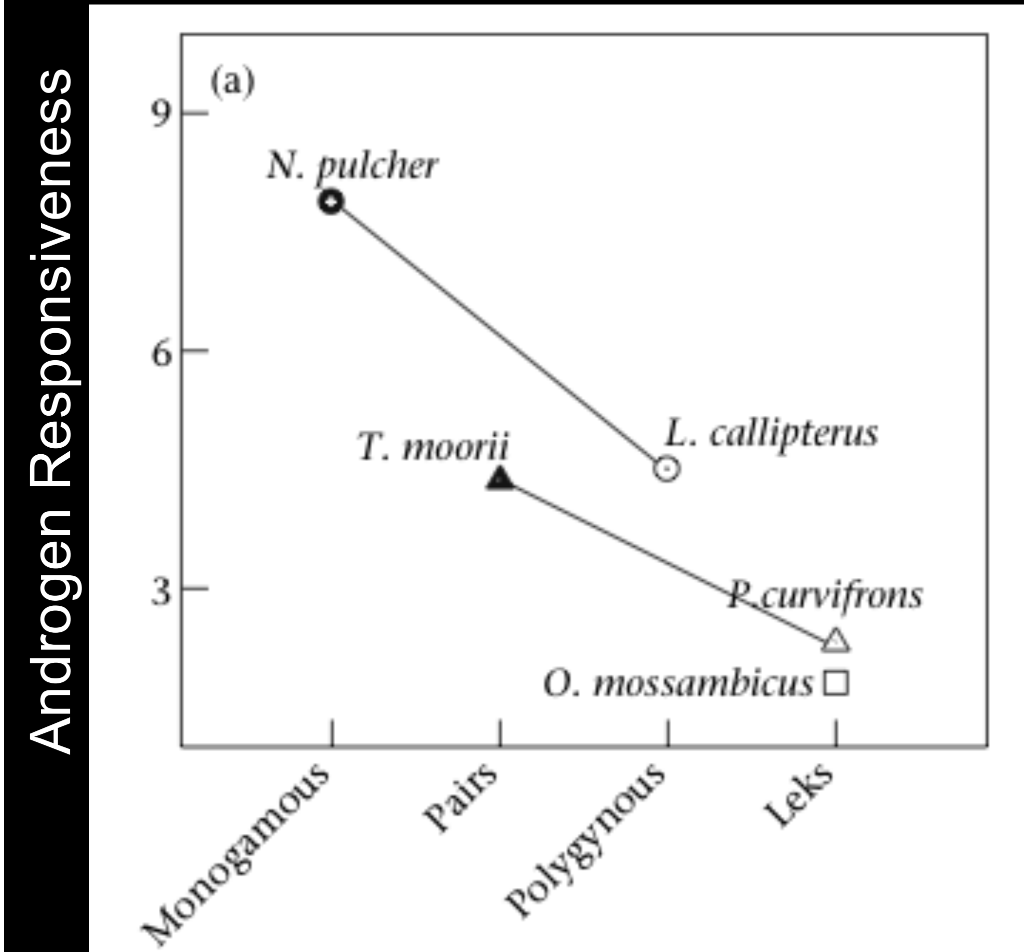
Lemur catta

Cavigelli, S.A., Pereira, M.E. (2000) Mating Season Aggression and Fecal Testosterone Levels in Male Ring-Tailed Lemurs. Hormones and Behavior 37:246-255.





Cavigelli, S.A., Pereira, M.E. (2000) Mating Season Aggression and Fecal Testosterone Levels in Male Ring-Tailed Lemurs. Hormones and Behavior 37:246-255.



N. Pulcher

T. Moori

L. Callipterus

P. Curvifrons

O. mossambicus

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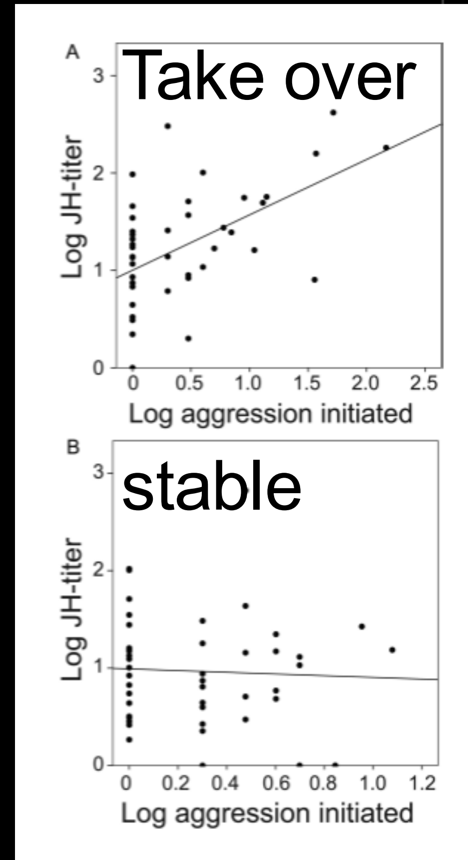

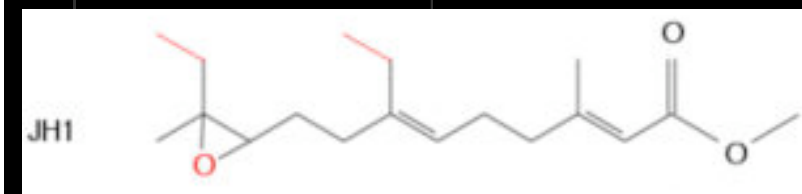

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Table 2
Correlation of hormonal variables with behavioral categories

	T1	T2	TC	C1	C2	CC
Threat	0.40*	0.29	−0.16	0.06	0.27	0.14
Fighting	0.45*	0.39*	−0.01	−0.05	0.30	0.39*
Domination	0.18	0.18	0.17	0.22	0.47*	0.11
Attack	0.54**	0.48*	−0.02	−0.001	0.32	0.40*
Defense	0.35	0.30	−0.06	−0.10	0.28	0.38

T1:Testosterone precombat levels, T2: testosterone postcombat levels, TC: testosterone changes, C1: cortisol precombat levels, C2: cortisol postcombat levels, CC: cortisol changes.

*$p < 0.05$.

**$p < 0.01$.

Behavioral observations

Behavioral categories	Elements included
Threat	—Stands erect without moving, looking hard at opponent —Runs into opponent —Extends, opens or lifts arms —Shouts
Fighting	—Both are struggling for an advantageous grasp (Kumi–Kata) but neither is dominant
Domination	—Grasps opponent and stands more erect, keeping adversary down —Moves the opponent pushing or pulling vigorously —Grasps adversary firmly
Attack/counterattact	—Standing up: tries to throw opponent (Nage–Waza) —On the ground: tries to immobilize (Osae–Waza), strangle (Shime-Waza) or apply an arm-lock (Kansetsu–Waza) —Standing up: when attacked applies a counter-technique (Kaeshi–Waza) —On the ground: moves to an offensive from a defensive position
Defense	—Stays dominated by opponent, while takes a defensive position standing or on the ground (face downwards, grasping opponent's leg or body) —Tries to avoid (Tai–Sabaki) or block the other's attacks —Simulates an attack without really trying to throw his opponent
Stop	—The referee halts the combat for technical reasons (Matte, Sonomama, or Soremade)
Observation	—Observes adversary, from a distance —Moves around opponent

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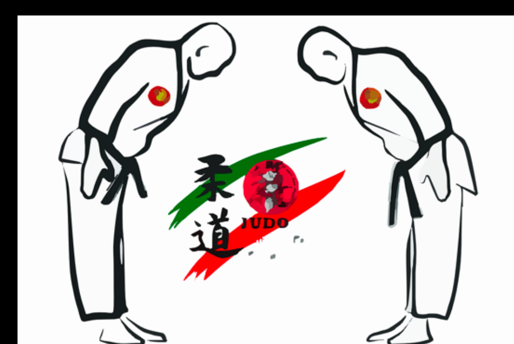

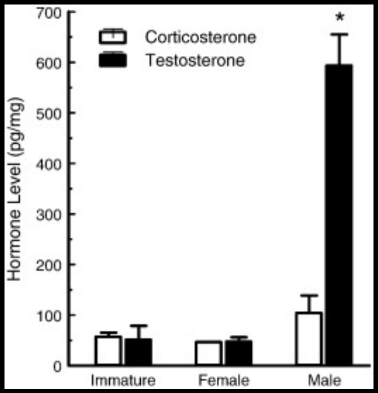

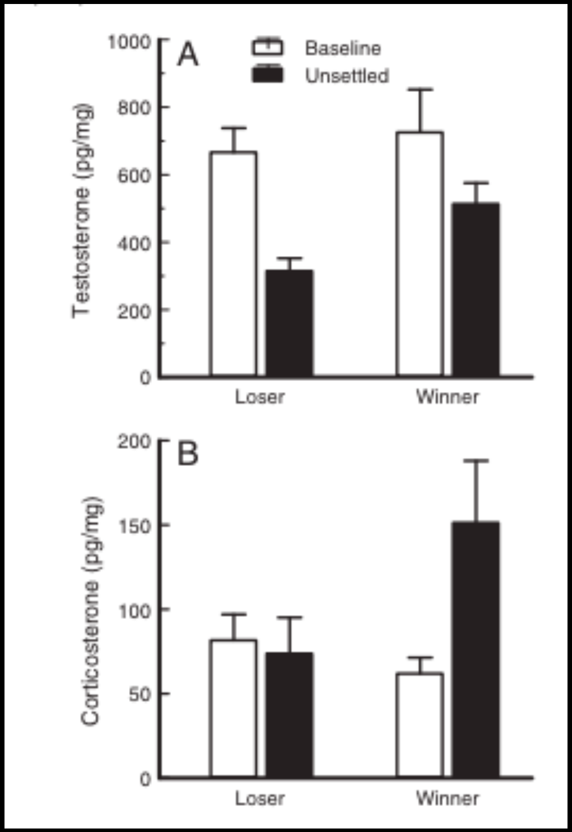

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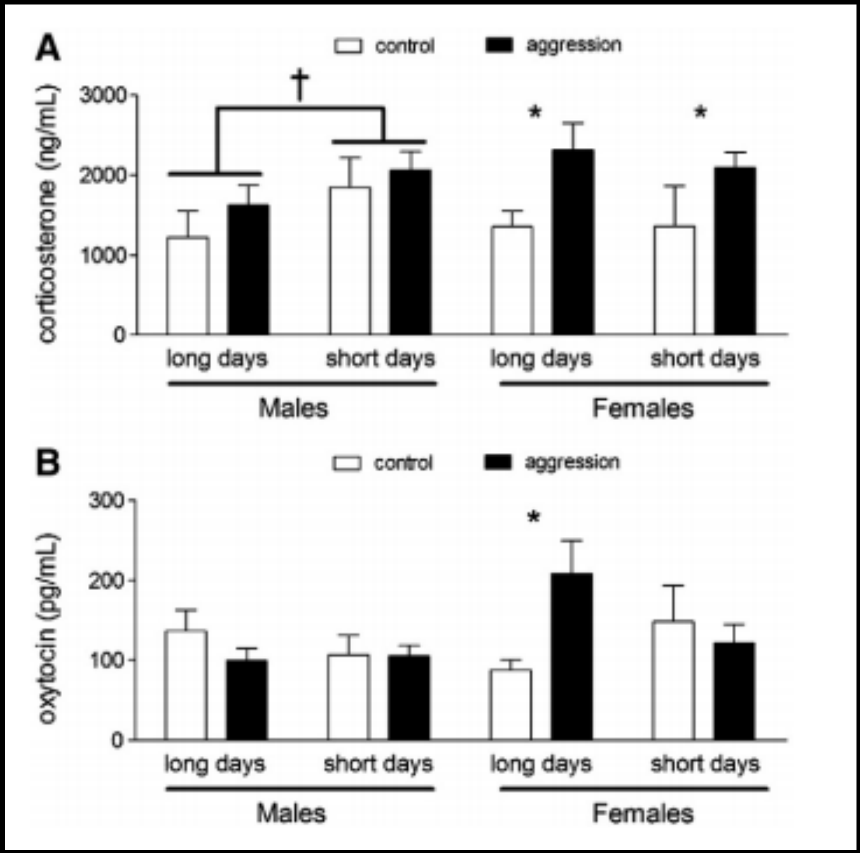

Sex differences in hormonal responses to social conflict in the monogamous California mouse

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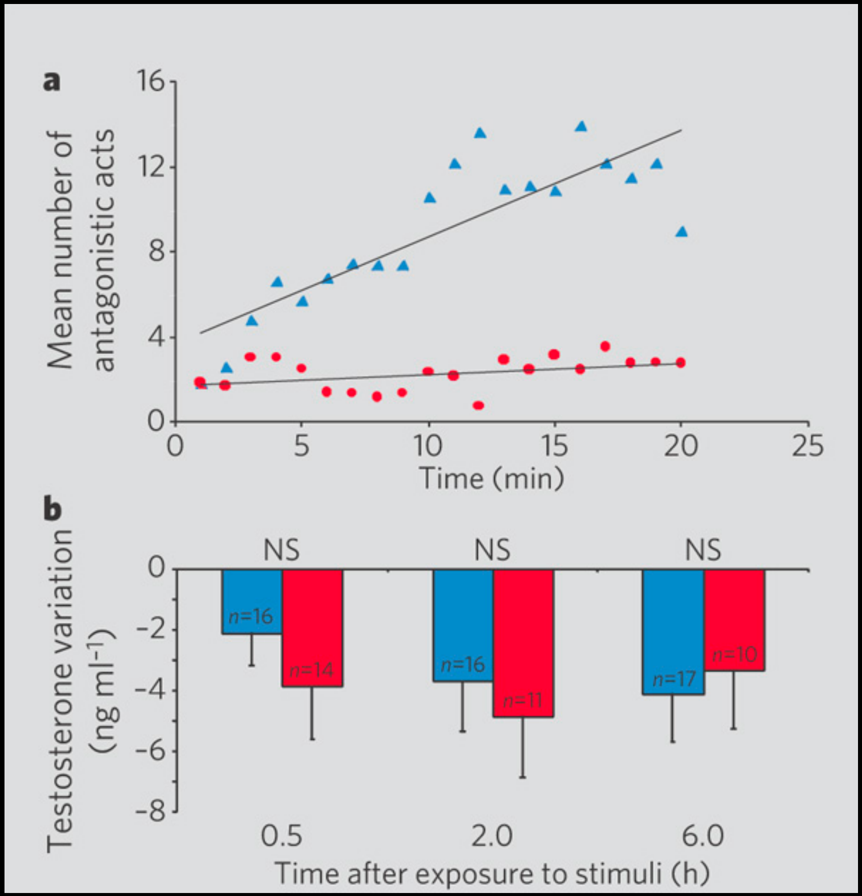

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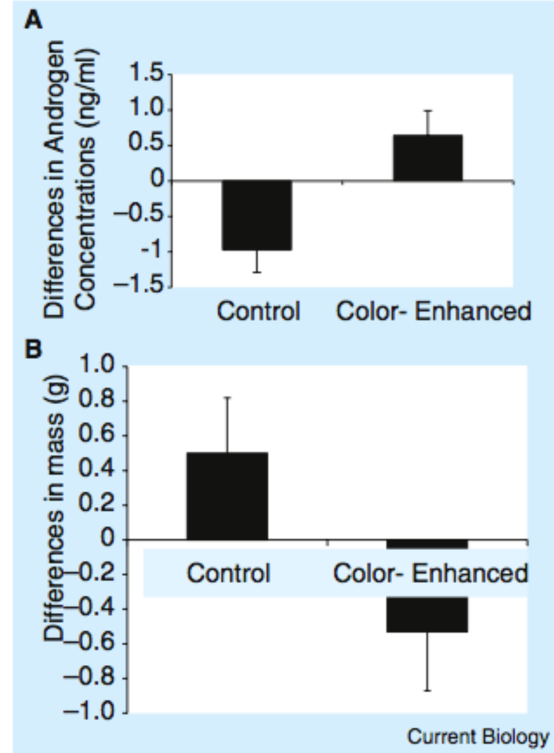

Figure 1. Color enhancement alters androgen levels and body mass of male barn swallows.

Sexual signal exaggeration affects physiological state in male barn swallows

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