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Alternative reproductive strategies in the ruff, *Philomachus pugnax*: a mixed ESS?

FREDRIK WIDEMO
Section of Animal Ecology, Department of Zoology, Uppsala University
and
Department of Zoology, Norwegian University of Science and Technology, Trondheim

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ABSTRACT

In the ruff, there are two alternative male reproductive strategies. The majority of males of this lekking bird attempt to establish and defend territories on leks, and are referred to as Independents. Other males, referred to as Satellites, forego this behaviour and instead attempt to get access to the territories defended by Independents by acting submissively. The system is thought to be an example of a mixed evolutionarily stable strategy (ESS), where the two strategies have equal fitness payoffs and are maintained by negative frequency-dependent selection. Satellites visited leks at the same time as females, and were associated with territory-holding Independents which were successful in attracting females. This appeared to be an effect both of Satellites following females, and of females being attracted to Independents that dominated submissive Satellites. Males pursuing the two strategies benefited from the presence of each other, at least to some extent. In this study, Satellites got fewer copulations than expected by their proportion in the population. Satellites on leks might have increased longevity or reproductive life span, and gained copulations off leks and while migrating, to compensate for their low observed mating success on leks. The Satellite strategy may be a low-cost, low-benefit strategy, which may have equal average lifetime reproductive success as the territorial strategy.

Animal mating systems show a remarkable variation between species, and some species even show plasticity in reproductive behaviours between, and within, populations (Emlen & Oring 1977). Distinct alternative male mating behaviours also sometimes co-occur within populations (e.g. Austad 1984; Gross 1984; Shuster 1989; Zimmerer & Kallman 1989). Authors have extensively applied game theory and the concept of evolutionarily stable strategies (ESS; Maynard Smith 1982) to alternative reproductive behaviours while attempting to explain how the strategies are maintained. Here, I define a strategy as a genetically based programme that governs the allocation of the somatic and reproductive effort of an organism. Thus, the strategy functions as a decision rule between alternative phenotypes, which are referred to as tactics (Gross 1996). Evolutionarily stable strategies may be divided into pure, conditional and mixed strategies (Maynard Smith 1982; Gross 1985). In a pure ESS, all individuals adopt the same genetically fixed tactic. Conditional strategies are composed of several tactics which provide unequal fitness payoffs, and are adopted by individuals depending on their competitive ability or status. Mixed strategies, finally, are different strategies that coexist and confer identical fitness payoffs to the individuals adopting them.

Most of the variation in reproductive behaviour within populations is nongenetic in its origin (Austad 1984), and even when there is a genetic component the majority of the strategies appear to be conditional and reversible. The most common occurrence of alternative strategies is various forms of sneaking behaviour where some males parasitize on the attractiveness of others (Waltz 1982). The sneakers are often young and competitively inferior males (Arak 1984; Zimmerer & Kallman 1989; but see Caro & Bateson 1986), which later in their lives will adopt a 'straightforward' mating behaviour and attract mates on their own. Sneakers occur primarily in species with a large variance in male mating success (Gadgil 1972; Shuster 1989), where, consequently, there is ample opportunity for sexual selection to act (Wade 1979; Wade & Arnold 1980).

In a few species alternative reproductive strategies appear to have become genetically fixed, however, and

Correspondence and present address: F. Widemo, Section of Animal Ecology, Department of Zoology, Villavägen 9, S-752 36 Uppsala, Sweden (email: fredrik.widemo@zoologi.uu.se).

individuals retain their adopted strategies throughout their lives. Although evidence is scant, examples come from a wide range of taxa: fish (Gross 1985; Zimmerer & Kallman 1989), insects (Cade 1981), isopods (Shuster 1989), and birds (Hogan-Warburg 1966; van Rhijn 1973, 1983). Negative density-dependent selection has been invoked to explain how the different strategies are maintained in populations (Maynard Smith 1982; Gross 1991; Shuster & Wade 1991). Thus, the alternative strategies are believed to constitute a mixed ESS, with equal fitness payoffs to individuals adopting the different strategies.

The ruff is the only bird, and indeed the only higher vertebrate, thought to have fixed alternative reproductive strategies. Two genetically determined male strategies exist (Hogan-Warburg 1966; van Rhijn 1991; Lank et al. 1995), but no one has yet been able to show conclusively how the two strategies are maintained in a population. In this paper, I describe in detail the interactions between males adopting the two strategies, and attempt to determine the mating success of the strategies. I also suggest how the two male reproductive strategies may be maintained in populations.

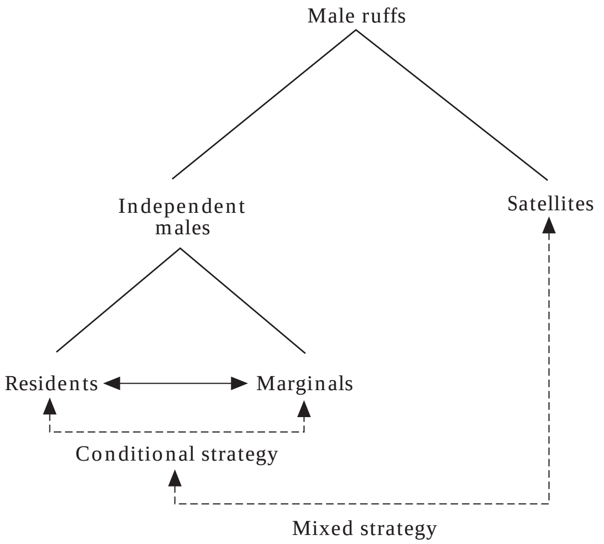

Figure 1. Schematic drawing of the alternative mating strategies in the ruff. The Independent and the Satellite strategies are fixed for life; transitions between Resident (territorial) and Marginal (floater) status may, however, occur within the Independent strategy. Thus, the Independent strategy constitutes a conditional strategy in itself, and the Independent and the Satellite strategies make up alternative strategies in what may be a mixed ESS.

METHODS

The Species

The ruff is a lekking wader which breeds throughout northern Eurasia. In this species, some males, referred to as Independents, attempt to establish and defend territories on leks, whereas other males, so-called Satellites, try to get access to territories defended by Independents. The Independents that succeed in establishing territories are called Residents, and the nonterritorial Independents are called Marginals (Hogan-Warburg 1966). The Marginals are potential future Residents which act as floaters in the population. Marginals may establish themselves on leks, either by ousting Residents from the leks or by setting up new territories. Thus, there are transitions between Resident and Marginal status within the Independent strategy both between and within years. By contrast, the Independent and the Satellite strategies appear to be fixed for life (Hogan-Warburg 1966; van Rhijn 1991; personal observations; Fig. 1). Only one transition between the two strategies has ever been reported, and this shift in behaviour was only temporary (van Rhijn 1991). There is also, however, a third group of males, which develops no male nuptial plumage. These males have been referred to as ‘naked-nape males’ by Hogan-Warburg (1966), and may attempt to get sneak copulations on the leks (personal observation). Whether this is a conditional or fixed strategy is not known. It is very rare to observe such males (less than 1% of the males are naked-napes; personal observation), and the importance of such males for the stability of the system remains unclear. For these reasons, I will not consider these males further.

Satellites are accepted on the territories of Residents as long as they act submissively, whereas Marginals are invariably chased to the outskirts of the leks. Satellites often form a tight association, here termed ‘coupling’, with Resident males. The Satellite will typically walk up to a Resident and squat right in front of him. The Resident responds by adopting a half-squat, usually holding his bill on the head or neck of the Satellite. Occasionally the Resident may peck at or above the head of the Satellite, who will remain in a submissive posture with his bill pointing towards the ground, or break up the coupling and leave. The Satellites usually initiate the association by approaching a Resident, but both the Resident and the Satellite will have to agree to form a coupling. Residents will normally only couple to Satellites inside their own territories, and Satellites can at any time terminate a coupling by moving away from the territory. Residents may evict Satellites from their territories by pecking very aggressively. Females typically visit several leks for 2–3 days and will often mate repeatedly with the same or different males (Lank & Smith 1987; Höglund et al. 1993). Females visit Residents on their territories and may or may not solicit copulations. If a Resident with a Satellite on his territory becomes distracted by an intruding neighbouring Resident as a female solicits, the Satellite may manage to steal a copulation.

Male ruffs are extremely polymorphic in the colour and pattern of the breeding plumage. This polymorphism is coupled to the dimorphism in behaviour, such that Satellites on average are paler than Independents (Hogan-Warburg 1966; van Rhijn 1991; personal observations). This makes it possible to determine the strategy adopted by a male from observations of behaviour and coloration, and to recognize individuals.

The Study

I studied a population of ruffs during the breeding seasons of 1990–1997. The study area comprises 410 ha of grazed shore meadows on the southern part of the island of Gotland in the Baltic Sea (57°10′N, 18°20′E). Males typically arrive from the wintering quarters before the females in mid–late April and lekking commences soon thereafter. The vast majority of the female visits and matings occur inside a 2–3-week period. Lekking occurs throughout the day, with a pronounced peak around dawn (Höglund et al. 1993; Widemo 1995).

In 1990–1992, I focused on determining the mating success for males adopting the different male reproductive strategies. Males were identified from colour rings, or from their polymorphic breeding plumages. All males observed were described in an attempt to determine the relative proportions of the two strategies in the population. How long males were present on the leks was noted, and all the copulations that occurred were recorded. In 1990–1992, 4–13 leks were observed at various times of the day at least every third day for as long as the leks remained active (range of annual observation time per lek 217–6627 min). In 1993, morning observations only were carried out on 12 leks (range of total observation time per lek 238–2782 min), but most Marginals were not described and the frequencies of the strategies in the population could not be determined. The length of the field season, and the proportion of observations during the morning peak, differed between years. The data on male behaviours were, therefore, restricted to morning observations from a 20-day period around the annual population mating peak. To avoid pseudoreplication, I based the analyses on data for individual males from one breeding season only. For each male, I chose the breeding season that had the largest observation time for the lek where he had been observed most often. I used data from the entire breeding season to increase sample sizes when comparing number of attempted, disrupted and successful copulations between the strategies.

In 1990–1993, 13–15 leks were active in the area and they could not all be observed at the same time. Residents only rarely visited more than one lek, and the proportion of observation time they were present on the lek where they were territorial therefore gives a good estimate of Resident lek attendance. Conversely, Satellites and Marginals frequently moved between leks, and could either have been present on another lek or have spent their time feeding when not present on one of the monitored leks. This made it impossible to calculate overall male lek attendance (time present on leks per observation time) for Satellites and Marginals with any accuracy. The lek attendance of individual males pursuing the Independent and the Satellite strategies could, consequently, not be compared. It was, however, possible to compare the relation between the total number of minutes spent on monitored leks by males adopting the different strategies and the observed frequencies of the strategies. Similarly, I could not compare the number of copulations per observation time between Independents and Satellites. The number of copulations performed per male while he was present on monitored leks could, however, be calculated and compared between the strategies.

I defined copulation attempts as instances when a male mounted a crouching female. Terminated copulation attempts were instances when a male mounted a soliciting female but she terminated the copulation attempt before cloacal contact had occurred. Male mountings that were terminated because of intervening males of either strategy were defined as disruptions. A copulation attempt was deemed successful if the mounting resulted in cloacal contact between the male and the female.

In 1994–1995 I examined in detail the interactions between males adopting the different strategies. Marginals that spent little time on the leks were not described, so I could not assess the relative proportions of the two strategies in the population during those 2 years. Male and female presence was monitored every 10 (1994) or 5 (1995) min during morning observation periods, and at the same time any occurrence of Resident–Satellite couplings was noted. Furthermore, females clearly inside the territories of Resident males during the counts were assigned to these males. The analyses were restricted to a 20-day period around the annual mating peak. Eight leks were monitored in 1994 (range of total per lek observation times: 250–1000 min), and six in 1995 (range of total per lek observation times: 155–780 min). Data on female and Satellite distributions on the leks were also collected in the same way in 1996 (six leks) and 1997 (seven leks). Thus, the analyses on distribution of females and Satellites were based on observations from eight leks and 4 years, yielding a total of 22 lek-years. I used randomization tests to investigate whether coupled Satellites and females preferentially associate with the same Residents. I tested the null hypothesis of no association between the distribution of females and Satellites using data from the subset of counts where at least one Resident was coupled and at least one female was assigned to a Resident ($N=245$ counts, all from different female visits). I compared the observed distribution of females and coupled Satellites with distributions generated in randomization simulations. All simulations were run 15 000 times; each iteration compared 22 observed and expected distributions, one from each observed lek and year.

As Satellites are free to move between leks, and frequently do so, I analysed Satellite distributions and behaviours across leks. As Residents spend almost all their time on one lek, I performed the correlational analyses of Resident behaviour within leks, and later combined them across leks using Fisher's combined probability test (Sokal & Rohlf 1995). Only leks where at least five copulations had been performed by Residents were included in the correlational analyses of Resident behaviours. There were no differences between years, and the data were therefore pooled over the study years. All behaviours were corrected for observation effort (expressed as behaviour per observation time) or expressed as rates (behaviour per male time present).

In 1994, I followed focal Satellites between the 10-min counts. I followed each Satellite for 30 min if it remained that long on a lek. After 30 min, or after the Satellite had left the lek, I chose another focal Satellite if there was one present. If no other Satellite was present after 30 min, I continued to follow the same one. In all, 42 Satellites were followed for a total of 2749 min I noted the

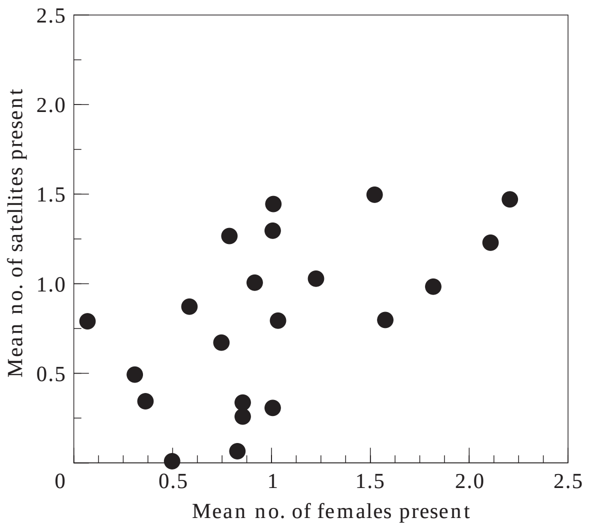

Figure 2. The relationship between the mean number of females and mean number of satellites present on a lek, exemplified by data from the lek with the largest number of observation periods in 1991 (r_S=0.56, N=21, P=0.01).

behaviour of the focal Satellites and, where appropriate, the behaviours of their coupled Residents continuously. The intensity of pecking by the Residents while coupled was scored on a three point scale: score 1 denotes pecking in the air above the head of the Satellite; score 2 denotes one to three pecks at the head; and score 3 denotes prolonged pecking at the head. These pecking scores were added up for Residents and Satellites and were corrected for the time each individual had been coupled and under focal study. All copulations occurring on the leks were recorded in 1994–1996, and whether the copulating male was coupled just prior to the copulation was noted. All statistical tests (except the *G* and chi-square tests) are two-tailed. For more detailed information on breeding area and observational methods see Höglund et al. (1993) and Widemo (1995).

RESULTS

Interactions Between the Male Strategies

There was a positive correlation between daily Satellite lek attendance (the total number of Satellite minutes spent on a lek corrected for observation time) and daily female attendance in 1990–1993 (combined Spearman rank correlations from 12 leks (r_S=0.29–0.87) using Fisher's combined probability tests: χ^2_{24}=123.6, P<0.0001; Fig. 2). Focal Satellites coupled with Residents immediately upon arriving at a lek more often when there were females present than when arriving at a lek without females present (Wilcoxon signed-ranks test: Z=2.69, N=12 Satellites arriving with and without females present, P=0.007). Also, established couplings on average lasted longer in the presence of females (Wilcoxon signed-ranks test: Z=2.35, N=12, P=0.02), and Satellites were less likely to leave the lek when females were present (Wilcoxon signed-ranks tests: Z=2.21, N=23, P=0.03). In 93% of all cases the arrival of females at a lek previously without females present elicited an immediate coupling by focal Satellites and Residents (N=77 cases), and the coupled pairs immediately terminated couplings in all cases when all the females left the lek (N=43 cases). This excludes all the cases where the Satellites left together with the females, which often happened. Thus, individual Satellites spent a larger proportion of their time on leks coupled to Resident males in the presence than in the absence of females (Wilcoxon signed-ranks test: Z=3.93, N=24, P<0.0001). Focal Satellites spent 42 ± 4.9% ($\bar{X}$ ± SE) of their time coupled on leks when there were females present, and 15.4 ± 7.1% of their time coupled when no females were present. Residents spent 14 ± 2.3% of their time coupled in the presence of females, and 3.6 ± 1.7% of their time coupled in the absence of females in the lek.

Females were found inside the territories of coupled Residents much more often than expected by chance (randomization test across 22 lek-years: total number of female visits=245, P=0.0007). Satellites that spent more time coupled on a lek, when females were present, spent a larger proportion of the time coupled associated with a Resident currently with females on his territory (r_S=0.46, N=39, P=0.003). Also, there was a positive correlation between the proportion of time spent coupled in the absence of females on the lek, and the proportion of time spent coupled to a resident with females when females were present (r_S=0.68, N=23, P=0.0003). Thus, Satellites that coupled a lot gained access to more females, and those Satellites that coupled in the absence of females were most successful in gaining close proximity to females when females were present on the lek.

In 1994–1995, Satellites gained copulations only when coupled to Residents (N=20 copulations), and females were never seen to solicit to solitary Satellites (i.e. Satellites not coupled to a Resident). Of 119 Resident copulations 51% occurred when the Resident was coupled to a Satellite. Residents with a high proportion of counts with females present on their territories got more copulations (combined Spearman rank correlations performed within leks (r_S=0.20–0.50, total N=81): χ^2_{10}=19.4, P<0.05). Satellites spent more time coupled with Residents that had a high proportion of counts with females present on their territories over the breeding season, both in the presence and in the absence of females on the lek (combined within lek analyses with females present (r_S=0.55–0.88, total N=75,): χ^2_{10}=46.2, P<0.001; females absent (r_S=0.31–0.64, total N=73): χ^2_{10}=19.2, P<0.05). There was a positive correlation between proportion of time spent coupled in the presence and in the absence of females on the lek for Residents (combined within lek analyses (r_S=0.18–0.69, total N=73): χ^2_{10}=25.61, P<0.005). Residents successful in obtaining at least one copulation had a higher copulation rate when coupled than when not coupled (Wilcoxon signed-ranks test: Z=2.14, N=23, P=0.03). There was a positive correlation between the proportion of counts coupled to a Resident and number of copulations per time present on the lek for individual Satellites (r_S=0.27, N=70, P=0.02).

Table 1. Percentage of males of different strategies/tactics and their percentage of copulations

Year	Residents	Resident copulations	Marginals	Marginal copulations	Satellites	Satellite copulations
1990	33.3	91.7	47.0	0	19.7	8.3
1991	25.2	83.3	56.3	3.5	18.5	13.2
1992	28.6	90.7	52.4	1.2	19.0	8.1
Mean	29.0	88.6	51.9	1.6	19.1	9.9

Focal Satellites that spent more time coupled suffered more peckings ($r_S=0.77$, $N=29$, $P<0.0001$), and Residents pecked coupled focal Satellites more per min when there were females present on the lek than when no females were present (Wilcoxon signed-ranks test: $Z=1.96$, $N=12$, $P=0.05$). Coupled Residents currently with females on their territories pecked more per min than when females were present on the lek but not on their own territories (Wilcoxon signed-ranks test: $Z=2.28$, $N=16$, $P=0.02$).

Focal Satellites shifted directly from being coupled to one Resident to another more often in the presence than in the absence of females on the lek (Wilcoxon signed-ranks test: $Z=2.20$, $N=11$, $P=0.03$). The Satellites shifted to another Resident more often if there were no females on the territory of the coupled pair than when females were present (Wilcoxon signed-ranks test: $Z=2.09$, $N=11$, $P=0.04$), and shifts were often initiated by females moving from a coupled pair. Vigorous pecking by Residents at coupled Satellites appeared to attract females to the coupled pairs. Looking at female movements towards coupled pairs, there was a nonsignificant tendency for the time between the pecking bout preceding the female's movement and the actual movement to be shorter than the time from the female's movement to the next pecking bout (Wilcoxon signed-ranks test: $Z=1.80$, $N=22$ coupled pairs, $P=0.07$). Similarly, the time between preceding pecking bouts and female solicitations was significantly shorter than the time from the solicitation to the next pecking bout (Wilcoxon signed-ranks test: $Z=2.02$, $N=5$ coupled pairs, $P=0.04$). These analyses were performed on data from 2-min time windows around female movements and solicitations to coupled pairs.

Maintenance of the Male Strategies

There was no significant difference in number of copulations per male time present between the Independent and Satellite strategies in 1990–1992 (combined Mann–Whitney *U* tests performed within years: $\chi^2_6=1.97$, NS). There was, however, a highly significant difference between the three groups of males when the Independent strategy was broken up into the Resident and Marginal subgroups (combined Kruskal–Wallis tests: $\chi^2_6>55.26$, $P<0.001$). Residents performed considerably more copulations per time present than Satellites (combined Mann–Whitney *U* tests: $\chi^2_6>21.09$, $P<0.005$) and Marginals (combined Mann–Whitney *U* tests: $\chi^2_6>55.26$, $P<0.001$), and the Satellites in turn had a higher copulation rate than Marginals (combined Mann–Whitney *U* tests: $\chi^2_6>34.49$, $P<0.001$).

In 1990–1992, the average percentage of Satellites in the population was 19.1% (Table 1). These percentages are based on all the observed males that stayed on leks long enough to be described with any accuracy, and include migratory birds visiting leks. To check the robustness of this result, all males that spent less than 2 h on leks were excluded. The Satellite proportion in this subset of males was 0.4% lower than the overall average. Of all the male time spent on leks in 1990–1992 (in all 2364 h), Residents accounted for 81%, Satellites for 11% and Marginals for 7%. The percentage of males belonging to the different strategies differed significantly from the percentage of minutes spent on leks (combined *G* tests performed within years ($G=4.47$–11.27): $\chi^2_6>30.4$, $P<0.001$), such that Independents spent more time on the leks than expected, and Satellites less. When the three groups of males were compared, Residents spent much more time on the leks than expected and both Satellites and Marginals spent less (combined *G* tests performed within years ($G=191.2$–1253.0): $\chi^2_6>41.44$, $P<0.001$).

Satellites got only 9.9% of the 534 copulations observed in 1990–1992 (Table 1), which is significantly less than would be expected from the Independent–Satellite proportions in the population (combined *G* tests performed within years ($G=4.68$–15.20): $\chi^2_6>33.62$, $P<0.001$). The very successful Residents constituted 29% of the population, and performed 89% of the copulations. In total, 954 copulations were observed in 1990–1996, and Satellites performed 9.0% of them. Thus, the proportion of copulations accruing to Satellites seems fairly stable. There were no differences between the Independent and Satellite strategies in the probability of females terminating copulations (*G* test: $G=1.68$, $N=82$, NS) or of copulations being disrupted by other males (*G* test: $G=2.86$, $N=67$, NS).

DISCUSSION

The ruff has one of the most spectacular and fascinating mating systems of all bird species studied. Even though the species has been intensively studied (e.g. Hogan-Warburg 1966; van Rhijn 1973, 1991), the fitness payoffs associated with different male reproductive behaviours remain obscure. In particular, it is unclear whether Residents and Satellites benefit from the presence of each other, whether the two strategies have equal fitness payoffs, and whether females sometimes prefer to mate with Satellites.

Interactions Between Male Strategies

In this study, female presence on the leks was clearly associated with the presence of Satellites, and Residents with Satellites on their territories also got more visits from females. There are at least four alternative explanations for the observed pattern of Satellites and females visiting leks at the same time and being associated with the same Residents. First, Satellites may simply track female movements on and between leks. Second, Satellites and females may prefer to visit the same Residents. Satellites may for example use the same criteria when choosing with whom to couple as the females use in mate choice. Third, coupled Residents may enjoy more female visits because females prefer to visit coupled pairs. Female ruffs mate with dominant Residents (Widemo 1997), and the Resident–Satellite coupling may function as a form of ritualized fight where the Resident is able to show his dominance over a submissive Satellite. Finally, the observed pattern could be explained by females tracking Satellite movements on the leks.

Satellites were often seen tracking female movements on the lek. Couplings were terminated when females left the leks, however, and the observed pattern of Satellites also being coupled to Residents preferred by females in the absence of females therefore cannot be explained only by Satellites tracking female movements. Roughly half the Residents' copulations were performed while they were coupled, and there was a positive relationship between the numbers of copulations performed while coupled and not coupled. This would seem to suggest that females also prefer the same Residents in the absence of Satellites. Also, Satellites preferred to couple with the same Residents when females were absent. The results are not conclusive evidence of females and Satellites having similar preferences for Residents, however, since the Satellites may have seen females being associated with certain Residents on previous visits and approached them expecting many females to be attracted in the future. Satellites clearly shifted in response to female movements on the lek, but females also appeared to be attracted to coupled pairs where the Resident displayed his dominance by pecking at the Satellite. The increased levels of Resident pecking at coupled Satellites in the presence of females could be an attempt to keep the coupled Satellites at bay. The analyses of the order of events do, however, suggest that the pecking behaviour of Residents may also serve to attract females. Females were never seen to shift in response to movements by focal Satellites between territories unless they coupled with a Resident, and in the 8 years of study females were almost never seen to solicit to uncoupled Satellites directly. This would seem to refute the suggestion that the observed pattern is an effect of females tracking the Satellite movements. There were no significant differences between the two strategies in number of disrupted copulations or number of copulations terminated by females. This does not, however, necessarily mean that the females do not discriminate against Satellites. The Satellites are remarkably quick to mount a soliciting female and complete a copulation if the coupled Resident is distracted by a neighbour. The copulation is over in less than a second, and in many cases females are probably not able to terminate the copulation before its completion.

My findings are in general agreement with the basis for the 'Resident's dilemma' model (Hugie & Lank 1997), where coupled pairs of Residents and Satellites act as 'leks within leks' and thereby attract females. Hugie & Lank suggested that Residents actively attempt to recruit Satellites, in order to increase the attractiveness of their courts. This may well be the case, but to test this critically in the field is probably impossible. Controlled mate choice experiments in captivity will be necessary to determine conclusively the female preferences for Residents, Satellites and coupled pairs.

Several of my analyses and results on the interactions between Residents and Satellites are similar to findings in previous studies of the ruff (e.g. Hogan-Warburg 1966; van Rhijn 1973). While many of the earlier studies are very impressive in their detailed descriptions of behaviours and interactions, most of them lack proper statistical testing of relationships and hypotheses. One of the few clear differences between the present study and previous work is the comparatively high proportion of Residents' copulations performed while they are coupled. van Rhijn (1991) found a much lower percentage of successful copulations for coupled Residents. One potential explanation for the discrepancy is differences in methodology. Here, Residents that were coupled when the females solicited and subsequently copulated were regarded as being coupled when copulating, regardless of whether the coupling was terminated as the Resident mounted the female, the rationale behind this being that the female had been attracted by and solicited to the coupled pair, rather than to a solitary male.

The continuous data from the focal Satellites proved difficult to analyse in several ways, and some of the results should therefore be treated with caution. Even if the human observers were convinced of the actions of males and females occurring in a certain sequence, the birds might have responded to cues of which we remained ignorant. For example, a Resident may be able to judge from the posture of a female that she is about to move in his direction, and this may elicit a pecking bout directed at his coupled Satellite. To the observer the female would appear to move in response to the male's action. In an attempt to minimize this problem only the cases that appeared clear cut were analysed and presented above.

In all, the results on interactions between the strategies suggest that the pattern of coupled Residents receiving more female visits and copulations is an effect both of Satellites tracking female movements and of female preferences for coupled pairs. Residents associated with conspicuous Satellites stand out, especially since the Residents may interact actively with the Satellites. Interacting with Satellites has definite advantages over interacting with other Residents, since Satellites, as opposed to Residents, never fight back. Satellites associate with

Residents in order to get access to females they cannot attract themselves, while Residents associate with Satellites to attract more females than they can when alone. Thus, males pursuing the two different strategies, at least to some extent, appear to benefit from the presence of each other.

Maintenance of Strategies in Populations

Explaining the evolution and maintenance of the two male reproductive strategies in the ruff has been a challenging task for behavioural ecologists for decades. Today, a convincing body of evidence exists for the life-long constancy of the two male behavioural strategies (Hogan-Warburg 1966; van Rhijn 1973, 1991, personal observations), and they have been shown to be genetically determined (Lank et al. 1995). The alternative strategies could not, therefore, be conditional with unequal fitness, or the fixed strategy with lower fitness would be outcompeted over evolutionary time. The Independent strategy appears to constitute a conditional strategy in itself, however, comprising the two status-dependent Resident and Marginal tactics. The alternative strategies of the Ruff are thought to be an example of a mixed ESS (Maynard Smith 1982) with identical, frequency-dependent, fitness payoffs to males pursuing the different strategies.

Van Rhijn (1991) compared the number of copulations per male time present on leks for males adopting the two strategies, and came to the conclusion that the Independents and the Satellites appeared to have identical success. Such comparisons of copulation rates cannot, however, be used for comparing the fitness accruing to males adopting the two strategies. The number of copulations per male time present may be of interest for discussing male allocation of time and energy, but the overall number of copulations (corrected for lek observation time rather than male time present) is the measure that should be used when discussing fitness consequences. Any comparison of the success of the two strategies must be based on absolute number of copulations, not copulations devalued to various degrees by the number of minutes each male, or strategy, has been present. Thus, the result of no significant difference between the number of copulations per min present between the two strategies in this study is in agreement with earlier work, but says nothing about the fitness of males adopting the strategies.

In the comparison of proportion of males belonging to the two strategies and the proportion of copulations performed, Satellites were less successful than Independents. Previous studies on the success of the male reproductive strategies in the ruff have yielded equivocal results. Working on the same Dutch population of ruffs, Hogan-Warburg (1966) and van Rhijn (1983, 1991) found that Satellites performed their expected proportion of copulations on some leks, but not on others. In an extensive study of a Finnish population, D. Lank (personal communication) failed to find any discrepancy between the proportion of Satellites in the population and the copulations accruing to them.

There are a number of factors that can affect the lifetime reproductive success of the two strategies such that Satellites and Independents may enjoy equal fitness payoffs even if males employing one strategy appear to copulate less. One potential explanation for the apparent discrepancy in mating success is that Satellites may be able to get more copulations off the leks (van Rhijn 1983, 1991; Lank & Smith 1987). Both Satellites and Marginals frequently followed females between leks and foraging sites, and often displayed to foraging females. It is impossible to follow such mixed groups of birds, since they are highly mobile. While observations at suitable foraging sites suggest that copulations off leks are very uncommon (personal observation), they do occur and may to some extent compensate for the low success of the Satellite strategy on the leks.

Females visit leks for several days to mate repeatedly with one or several males (Lank & Smith 1987; Höglund et al. 1993), and multiple paternity has been shown to be common in another population of ruffs (T. Burke, personal communication). Thus, sperm competition is likely to affect the success of individual males and of the strategies. Multiple copulations frequently occurred within a very limited time frame; in one case a Resident copulated 10 times inside 2 min with three females. By contrast, Satellites very rarely engaged in repeated copulations (personal observation). Copulating has been shown to reduce the ejaculate size of birds in subsequent copulations (Birkhead 1991; Birkhead & Møller 1992), and sperm depletion therefore probably also affects the success of male ruffs. Furthermore, males may modify ejaculate size, depending on the probability of the female already being inseminated and the probability of both the male and the female copulating in the future (Parker 1990a, b). Satellites copulate less often, and may therefore have larger ejaculates. This could lead to differences in the probability of paternity from copulations depending on the male's strategy.

Males of the two categories may also differ in longevity. Vacated Resident territories get taken up by other males very quickly (personal observation) and Residents have to defend their territory actively. Males are prevented from eating and drinking while on the lek, and Residents that spend the better part of the day on the leks for weeks on end are subject to considerable energetic stress. Satellites do not defend territories, and are therefore emancipated from having to spend time on the lek in the absence of females. Consequently, they are not subject to the same energetic stress as Residents (F. Widemo, G. Bachman & J. Höglund, unpublished data), and also have ample feeding opportunities as they follow females to foraging sites. This is reflected in the lower lek attendance of the Satellites. Differential mortality due to the differences in energetic stress is a distinct possibility. Furthermore, the reproductive life span may differ between the two strategies even in the absence of a difference in longevity. Males pursuing the Independent strategy more or less depend on the acquisition of a territory on a lek for their mating success. This creates a definite 'success-threshold' which is absent for the Satellites. It is, therefore, possible that Satellite males begin reproducing at an earlier age.

Similarly, Independents are unlikely to copulate while migrating since they depend on territory defence for their success, whereas the Satellites are probably accepted on leks and are more likely to get copulations while migrating than Independents are.

To conclude, both Residents and Satellites may benefit from interacting with each other on the leks. Males pursuing either of the two strategies clearly enjoyed different mating success on the leks in the ruff population under study, however. Even so, the alternative strategies probably do constitute a mixed ESS. The Satellite strategy may represent a low-cost, low-benefit strategy, and there are a number of factors that may compensate for the apparently low mating success of Satellites in terms of lifetime reproductive success.

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References

Arak, A. 1984. Sneaky breeders. In: *Producers and Scroungers* (Ed. by C. J. Barnard), pp. 154–194. London: Croom Helm.

Austad, S. N. 1984. A classification of alternative reproductive behaviors and methods for field testing ESS models. *American Zoologist*, **24,** 309–319.

Birkhead, T. R. 1991. Sperm depletion in the Bengalese finch, *Lonchura striata*. *Behavioral Ecology*, **2,** 267–275.

Birkhead, T. R. & Møller, A. P. 1992. *Sperm Competition in Birds*. London: Academic Press.

Cade, W. H. 1981. Alternative male strategies: genetic differences in crickets. *Science*, **212,** 563–564.

Caro, T. M. & Bateson, P. 1986. Organization and ontogeny of alternative strategies. *Animal Behaviour*, **34,** 1483–1499.

Emlen, S. T. & Oring, L. W. 1977. Ecology, sexual selection, and the evolution of mating systems. *Science*, **197,** 215–223.

Gadgil, M. 1972. Male dimorphism as a consequence of sexual selection. *American Naturalist*, **106,** 574–580.

Gross, M. R. 1984. Sunfish, salmon, and the evolution of alternative reproductive strategies and tactics. In: *Fish Reproduction: Strategies and Tactics* (Ed. by G. W. Potts & R. J. Wootton), pp. 55–75. London: Academic Press.

Gross, M. R. 1985. Disruptive selection for alternative life histories in salmon. *Nature*, **313,** 47–48.

Gross, M. R. 1991. Evolution of alternative reproductive strategies: frequency-dependent sexual selection in male bluegill sunfish. *Philosophical Transactions of the Royal Society of London, Series B*, **332,** 59–66.

Gross, M. R. 1996. Alternative reproductive strategies and tactics: diversity within sexes. *Trends in Ecology and Evolution*, **11,** 92–98.

Hogan-Warburg, A. J. 1966. Social behavior of the ruff, *Philomachus pugnax*. *Ardea*, **54,** 108–229.

Höglund, J., Montgomerie, R. D. & Widemo, F. 1993. Costs and consequences of the variation in the size of ruff leks. *Behavioral Ecology and Sociobiology*, **32,** 31–39.

Hugie, D. M. & Lank, D. B. 1997. The Resident's dilemma: a female choice model for the evolution of alternative mating strategies in lekking male ruffs (*Philomachus pugnax*). *Behavioral Ecology*, **8,** 218–225.

Lank, D. B. & Smith, C. M. 1987. Conditional lekking in the ruff. *Behavioral Ecology and Sociobiology*, **20,** 137–145.

Lank, D. B., Smith, C. M., Hanotte, O., Burke, T. & Cooke, F. 1995. Genetic polymorphism for alternative mating behaviour in lekking male ruff *Philomachus pugnax*. *Nature*, **378,** 59–62.

Maynard Smith, J. 1982. *Evolution and the Theory of Games*. Cambridge: Cambridge University Press.

Parker, G. A. 1990a. Sperm competition: raffles and roles. *Proceedings of the Royal Society of London, Series B*, **242,** 120–126.

Parker, G. A. 1990b. Sperm competition: sneaks and extra-pair copulations. *Proceedings of the Royal Society of London, Series B*, **242,** 127–133.

van Rhijn, J. G. 1973. Behavioural dimorphism in male ruffs, *Philomachus pugnax*. *Behaviour*, **47,** 153–228.

van Rhijn, J. G. 1983. On the maintenance and origin of alternative strategies in the ruff *Philomachus pugnax*. *Ibis*, **125,** 482–498.

van Rhijn, J. G. 1991. *The Ruff*. London: T. & A. D. Poyser.

Shuster, S. M. 1989. Male alternative reproductive strategies in a marine isopod Crustacean (*Paracercis sculpta*): the use of genetic markers to measure differences in fertilization success among α-, β-, and γ-males. *Evolution*, **43,** 1683–1698.

Shuster, S. M. & Wade, M. J. 1991. Equal mating success among male reproductive strategies in a marine isopod. *Nature*, **350,** 608–610.

Sokal, R. R. & Rohlf, F. J. 1995. *Biometry*. 3rd edn. New York: W. H. Freeman.

Wade, M. J. 1979. Sexual selection and variance in reproductive success. *American Naturalist*, **114,** 742–746.

Wade, M. J. & Arnold, S. J. 1980. The intensity of sexual selection in relation to male sexual behaviour, female choice and sperm precedence. *Animal Behaviour*, **28,** 446–461.

Waltz, E. C. 1982. Alternative mating tactics and the law of diminishing returns: the satellite threshold model. *Behavioral Ecology and Sociobiology*, **10,** 75–83.

Widemo, F. 1995. Distribution models and the evolution of lekking with empirical tests on the ruff, *Philomachus pugnax*. Ph.D. thesis, Uppsala University.

Widemo, F. 1997. The social implications of traditional use of lek sites in the ruff, *Philomachus pugnax*. *Behavioral Ecology*, **8,** 211–217.

Zimmerer, E. J. & Kallman, K. D. 1989. Genetic basis for alternative reproductive tactics in the pygmy swordtail, *Xiphophorus nigrensis*. *Evolution*, **43,** 1298–1307.