

The resident's dilemma: a female choice model for the evolution of alternative mating strategies in lekking male ruffs (*Philomachus pugnax*)

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Previous models for the evolution of alternative male mating behavior have virtually ignored the role of female choice. We present a model in which female choice favors the evolution and maintenance of alternative mating strategies in male ruffs, *Philomachus pugnax*. Resident male ruffs establish and defend courts on leks against other residents, while non-territorial satellite males move between leks and among courts on a lek. Residents appear to actively recruit satellites to their courts, even though satellites may mate with females once there. Resident behavior toward satellites and data on female behavior suggest that residents benefit from a satellite's presence due to some female preference for mating on co-occupied courts. However, if all residents accept satellites, none gains any relative advantage, yet all pay the costs of having satellites on their court. We present a game theoretical model that shows that the relative nature of female choice places residents in an evolutionary dilemma with respect to satellite acceptance. Although all residents would benefit if satellites could be cooperatively excluded from leks, the only evolutionarily stable strategy for individual residents is to defect and accept satellites. The model also demonstrates that this "resident's dilemma" likely exists only in a local sense, since the failure of residents to cooperatively exclude satellites from leks need not result in globally lower payoffs, due to frequency-dependent selection on the proportion of satellites in the population. Our analysis suggests that the resident-satellite relationship in ruffs, despite its obvious competitive elements, is fundamentally a cooperative association favored by female choice. Female choice has also been proposed as the primary mechanism selecting for male association to form leks in ruffs. In this context, resident-satellite associations may be thought of as transitory "leks within a lek." **Key words:** alternative mating strategies, cooperation, female choice, game theory, leks, *Philomachus pugnax*, polymorphism, prisoner's dilemma, ruffs, sexual selection. [*Behav Ecol* 8:218–225 (1997)]

Why do unrelated males of some species form associations while competing for mates? This question has been considered in depth in discussions of the evolution of leks, a striking example of close association among competing males (e.g., Bradbury and Gibson, 1983; Clutton-Brock et al., 1993; Höglund and Alatalo, 1995; Wiley, 1991). Hypotheses for why leks occur differ fundamentally in the nature of the proposed relationships among participating males. Some models emphasize mutual benefits for males due to female preference for mating within male aggregations (female choice models: Bradbury, 1981; Gibson et al., 1990; Lank and Smith, 1992; Queller, 1987; Wrangham, 1981; black hole models: Clutton-Brock et al., 1992) or due to decreased predation risk relative to solitary display (Gosling, 1986; Lack 1968; Wittenberger, 1978). Several models imply a neutral relationship among males, suggesting that individual males simply assemble independently at sites with above average encounter rates with females (hot-spot models: Balmford et al., 1993; Bradbury, 1981; Lank and Smith, 1987; Westcott, 1994). Finally, other models propose that leks result from lower status males parasitizing higher status males by clumping around them and intercepting females (hotshot models: Arak, 1983; Beehler and Foster, 1988; Höglund and Robertson, 1990; Waltz, 1982; Widemo and Owens, 1995). It has proved difficult to determine the relative importance of these mechanisms in favoring

male association at leks in different species (Clutton-Brock et al., 1993; Höglund and Alatalo, 1995; Wiley, 1991).

In many species, associations also occur between competing males with alternative mating behaviors (Arak, 1984; Austad, 1984; Gross, 1996; Taborisky, 1994). Examples include nondisplaying "satellite" males that surround displaying males and intercept approaching females (e.g., bullfrogs, *Rana catesbeiana*: Howard, 1981, 1984), and "sneakers" or "female mimics" that place themselves near the nests of territorial males and attempt to fertilize the eggs laid there by spawning females (e.g., sunfish, *Lepomis macrochirus*: Dominey, 1981; Gross, 1982). These associations are usually interpreted as parasitism of displaying or territorial males (Arak, 1984; Gross, 1996), and in this sense parallel the hotshot mechanisms proposed for the evolution of leks.

The ruff (*Philomachus pugnax*) is an Old World sandpiper that breeds across the lower Palearctic from England to Siberia (Cramp and Simmons, 1983; Scheufler and Stiefel, 1985; van Rhijn, 1991). The mating system of the ruff is unique among animals in having both well-developed leks and an intriguing association within leks between males with alternative mating strategies (Hogan-Warburg, 1966; van Rhijn, 1973, 1991). All males pursue one of two genetically determined mating strategies over their entire lifetime (Lank et al., 1995), each with associated plumage patterns. The majority of males are termed "independents" or "residents" when they defend approximate 1.5-m² lek mating courts against other residents (Hogan-Warburg, 1966). The remaining males are nonterritorial "satellites" that move between leks while tracking female movements (Lank and Smith, 1987). At a lek, satellites

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Table 1
Resident male ruff behavior toward satellites

Situation on court	Resident's behavior	Interpretation
Satellite nearby, female absent	Courtship displays: "half-squats," "full squats"	Recruit satellite onto court
Satellite and female present	"Mutual squats": resident in "forward" posture above satellite	Control, but not evict satellite
Satellite mates, tries to mate, or interrupts resident's mating	Resident attacks satellite with bill or feet	Use aggression to regain control of or evict satellite

gain access to a resident's court, where both males display to females, who may mate with either male.

Although satellites do not threaten a resident's possession of a court, their presence has significant reproductive costs. The most apparent cost is that satellites may mate with females that visit a resident's court. Satellites also interfere with the resident's matings, both directly, by disrupting the resident's mating attempts, and indirectly, by causing residents to miss

mating opportunities while interacting with satellites (Shepard, 1975; van Rhijn, 1973, 1991). This raises the obvious question of why resident males do not exclude satellites from their courts. No clear answer emerges from either the ethological literature (Hogan-Warburg, 1966, 1993; van Rhijn, 1973, 1991) or from previous theoretical discussions (e.g., Andersson, 1994; Caro and Bateson, 1986; Höglund and Alatalo, 1995; Maynard Smith, 1982; van Rhijn, 1983, 1985; Wiley, 1991).

We provide an explanation of this phenomenon by first reviewing and reinterpreting resident behavior toward satellites. We argue that resident behavior and field data on the behavior of females suggest that residents benefit from having satellites on their courts due to some female preference for mating on co-occupied courts. However, the relative nature of such a benefit means that if all residents accept satellites, none gains any relative advantage, yet all pay the costs, for having satellites on their court. We then present a "resident's dilemma" model which shows that the relative nature of female choice places residents in an evolutionary dilemma with respect to satellite acceptance. While all residents would benefit if satellites could be cooperatively excluded from leks, the only evolutionarily stable strategy for individual residents is to defect and accept satellites. Our model superficially resembles the prisoner's dilemma (Axelrod and Hamilton, 1981), the standard paradigm for the difficulties in achieving cooperation in a game-theoretical setting. However, unlike in the prisoner's dilemma, failed cooperation to exclude satellites need not result in globally lower reproductive payoffs for residents due to frequency-dependent selection on the proportion of satellites in the male population.

Resident behavior toward satellites

The behavioral interactions between residents and satellites include cooperative and competitive elements (Table 1; Hogan-Warburg, 1966; van Rhijn, 1973, 1991). When only satellites are near a court, residents usually stand motionless in a "half squat" with their bill pointed downward (Figure 1a), just as they do to court females (Figure 1b). This contrasts sharply with the agonistic "forward" position used when other resident males approach, in which a horizontal bill is pointed toward the intruder, often accompanied by "bill thrusts" or a charge. If a satellite joins the resident on the court, the resident male may drop into a "full squat," again, just as he does when a female approaches. Such behavior suggests that residents actively recruit satellites onto their courts.

When females are on or near a co-occupied court, the resident and satellite(s) usually enter into a "mutual squat" ("twosomes," Hogan-Warburg, 1966; "dyads," Höglund et al., 1993). The resident typically stands above the satellite and adopts the forward posture, but its bill sits over the satellite's head rather than being pointed at an opponent (Figure 1c; see also Hogan-Warburg, 1966:Figure 16). The resident may rotate partly around, bill-thrust over, or appear to peck at the satellite's head. A resident in this position may be able to pre-

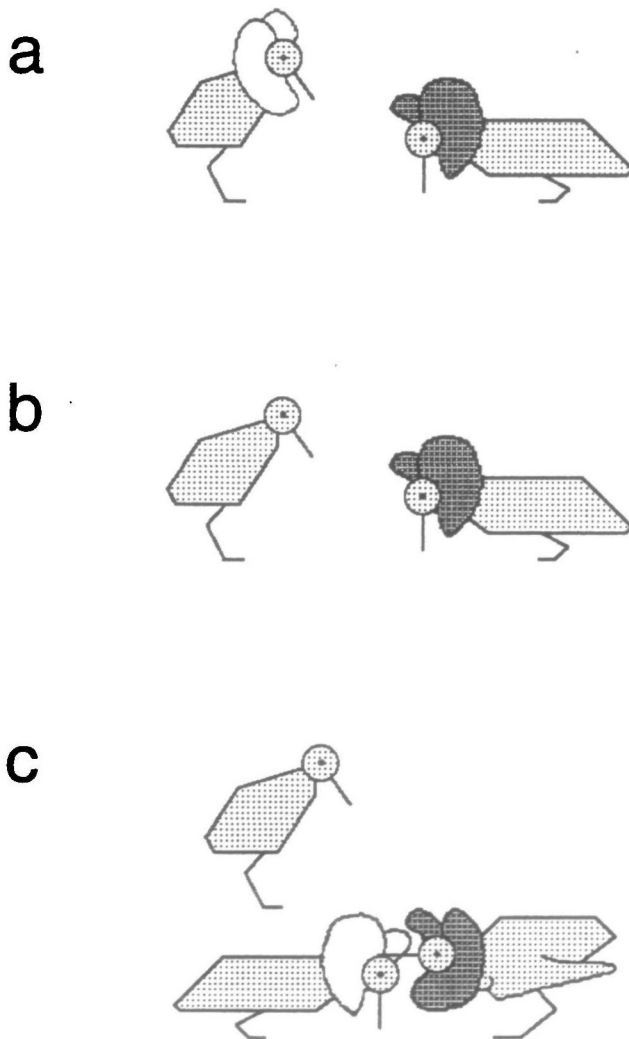


Figure 1
Typical postures adopted by resident male ruffs (with shaded ruffs) on mating courts: "half squats" when (a) a satellite or (b) a female is nearby, and (c) a "mutual squat" on a co-occupied court when a female is nearby. Adapted from van Rhijn (1991).

vent a satellite from rising from the squat to mate with a soliciting female. Thus, it appears that residents attempt to control satellites when females are present, but not evict them from the court.

If satellites mate, attempt to mate, or interrupt resident matings, residents typically attack satellites by jumping on them and kicking at their backs, and/or pecking at the top of their heads. Satellites react by squatting on the court without fighting back or by leaving the court (Hogan-Warburg, 1993). Thus, residents appear willing to use aggression to regain control of satellites, but they evict them only as a last resort.

Van Rhijn (1973, 1991) dichotomized resident behavior toward satellites as "tolerant" when females were not present versus "not tolerant" when females were present. We emphasize that residents do not merely tolerate satellites, but appear to actively recruit them onto their courts. Furthermore, most intolerant behavior appears to be an attempt to control rather than to evict satellites. Such behavior suggests that resident males benefit from having a satellite on their court, even though they are reproductive competitors that must be controlled; residents are not simply making the "best of a bad job" by accepting satellites (e.g., Höglund and Alatalo, 1995; Waltz, 1982).

How does a resident benefit from having a satellite on his court?

Several potential benefits to residents from having satellites on their court have been suggested. Most consider reproductive benefits, but satellites might act as predator sentinels (sensu Phillips, 1990) or as decoys (Sherman P, personal communication), increasing the probability of resident survivorship in return for a share of court matings. The latter case might imply different life histories for satellites and independents, for which no data are available. The only two observations of predation at ruff leks known to us specify that "white" birds were taken (Grosskopf, 1968:105; Männikkö, 1989). Although satellites typically have white plumages, independents also may have white neck ruffs, but with dark head tufts (Hogan-Warburg, 1966).

Resident males could benefit if satellites recruit females to the lek (Hogan-Warburg, 1966; van Rhijn, 1983). Satellite and female visitation rates do correlate positively among leks (Höglund et al., 1993). However, this correlation could reflect the fact that satellites often accompany females moving between leks. Van Rhijn (1973, 1991) found no difference in female visitation rate in a paired comparison of the same leks when satellites were or were not already present. In addition, Lank and Smith (1992; unpublished data) failed to find higher rates of female visitation when satellites were part of experimental leks, controlling for lek size and male composition. More fundamentally, such a lek-level benefit does not explain why individual residents appear to actively recruit satellites onto their court and incur the associated costs.

The most plausible benefit to a resident from having a satellite on his court is that females prefer to mate on courts occupied by satellites (Hogan-Warburg, 1966; van Rhijn, 1973). Such a benefit would explain why individual residents recruit satellites onto their court and are reluctant to evict them. All relevant studies report a strong positive relationship between the frequencies of satellite and female visits to resident males' courts (Hogan-Warburg, 1966, 1993; Lank DB and Smith CM, unpublished data; Shepard, 1975; van Rhijn, 1973, 1991). In a detailed analysis, van Rhijn (1973:197, 1991:76) found higher rates of female movement toward courts when satellites were present than when they were not. In contrast, satellite movements in response to female presence were

not detected. Residents with higher rates of satellite visitation over a season also had higher copulation rates within a lek, controlling for a suite of other variables (Hill, 1991). Although these observational data do not fully control for other underlying causes, they do support a benefit to residents based on female preference for mating on co-occupied courts.

The magnitude of any benefit to residents based on increased court attractiveness to females will depend on the frequency with which other residents accept satellites and thereby increase the attractiveness of their court. We now present a frequency-dependent model for the evolution of the alternative mating strategies of male ruffs based on female choice.

The resident's dilemma model

Consider the evolutionary game in which males pursue one of three possible breeding strategies (i). Males may be "satellites" ($i = s$), "excluding residents" ($i = e$) that chase satellites off their courts, or "accepting residents" ($i = a$) that recruit satellites to their courts. Satellite acceptance entails the costs of mating interference and sharing court matings with satellites. The strategy frequencies in the population are most conveniently described by the proportion of residents accepting satellites, p_a , and the proportion of males that are satellites, P_s . We assume that all males have similar life histories and therefore that p_a and P_s apply to both breeding males and the male population as a whole.

Reproductive payoffs

We assume that females assess the attractiveness of residents' courts and prefer to mate on courts with high attractiveness relative to others in the population. Court attractiveness is an absolute measure of the qualities of a court, including the males themselves, that females use to decide where to mate. Let $C(e)$ and $C(a)$ be the attractiveness of an excluding or accepting resident's court, respectively. The number of females successfully mated on the court of a resident male playing strategy i , $F(i)$, will depend on the breeding sex ratio, S (males/females), the proportion of satellites in the population, P_s , and how females choose among courts based on their relative attractiveness. For simplicity, we assume that $F(i)$ is proportional to a court's attractiveness, in which case:

$$F(i) = \frac{C(i)}{\bar{C}(1 - P_s) S}, \quad (1.0)$$

where \bar{C} is the mean court attractiveness given by:

$$\bar{C} = p_a C(a) + (1 - p_a) C(e).$$

The reproductive payoff, $R(i)$, for a resident male playing strategy i will be the product of the number of matings on his court [$F(i)$] and the proportion of those matings he obtains, M_i . We assume that M_a , for accepting residents, is constant ($0 < M_a < 1$) but acknowledge that the partitioning of matings between satellites and accepting residents is a game and a source of conflict between them when females are present. Although several satellites may co-occupy a resident's court, for simplicity we present our model in terms of single satellites. We assume that excluding residents are responsible for all matings on their courts ($M_e = 1$). Hence, the reproductive payoffs of the two resident strategies are:

$$R(a) = M_a F(a) \quad (2.1)$$

and

$$R(e) = F(e). \quad (2.2)$$

We assume that satellites obtain matings only on courts of

accepting residents. The reproductive payoff of the satellite strategy, $R(s)$, is then given by:

$$R(s) = \frac{p_a (1 - P_s)}{P_s} (1 - M_a) F(a). \quad (2.3)$$

Invasion of satellite acceptance among residents

We assume that ancestral ruffs had a typical avian lek mating system in which all breeding males were excluding residents. Given these initial conditions, it is difficult to imagine how a pure satellite strategy could invade without the prior existence of sufficient numbers of accepting residents. As discussed later, satellite behavior may have originally been part of a condition-dependent or opportunistic male strategy. For simplicity here, we assume some proportion of males, P_s , are willing to behave as satellites.

The accepting strategy will invade if it has a greater reproductive payoff than the excluding strategy:

$$R(a) > R(e). \quad (3.0)$$

Substituting from Equations 2.1 and 2.2 yields the following "invasion condition":

$$M_a F(a) > F(e). \quad (3.1)$$

Because $0 < M_a < 1$, satellite acceptance can invade only if it results in a net increase in the number of females mated on the court, taking into account mating interference by satellites, sufficient to offset the reduction in the proportion of court matings the resident obtains. From Equation 1.0, any increase in $F(a)$ relative to $F(e)$ must be due to an increase in the attractiveness of an acceptor's court [$C(a)$] relative to an excluder's [$C(e)$]. Because we assumed that females choose among courts such that $F(i)$ is proportional to $C(i)$, these two terms are interchangeable in Expression 3.1, but this need not be the case generally. Regardless, given our expression for $F(i)$, the invasion condition is not affected by the value of p_a and, if met, will lead to the eventual fixation of the accepting strategy by residents, despite a reduction in their reproductive payoff. In the unlikely case that Expression 3.1 was an equality, accepting and excluding residents would receive the same payoff and p_a would be neutrally stable and subject to stochastic processes, such as genetic drift.

To illustrate the dependence of resident payoffs on the frequency with which they accept satellites, we provide an example for which the invasion condition is met. We assume some constant proportion of males (P_s) behave as satellites. We arbitrarily chose values so the attractiveness of an acceptor's court [$C(a) = 2$] exceeds that of an excluder's [$C(e) = 1$], and assume an equal breeding sex ratio ($S = 1$). We chose a value for the proportion of court matings obtained by an accepting resident ($M_a = 0.84$) approximating that observed in the wild (Lank DB, Smith CM, unpublished data). Figure 2 plots the reproductive payoff to an accepting [$R(a)$] and excluding [$R(e)$] resident, the mean reproductive payoff to all residents, \bar{R} , (indicated by the dashed line), and the mean court attractiveness in the population (\bar{C}) as a function of the proportion of residents accepting satellites (p_a). The vertical scale of the reproductive payoff panel will depend on the value of P_s and is arbitrarily scaled so that the payoff to residents when all exclude satellites (i.e., $p_a = 0$) is 1.

As the accepting strategy spreads among residents, two important changes occur. First, mean court attractiveness (\bar{C}) increases because an increasing proportion of courts are co-occupied. As this happens, the relative advantage for an accepting resident over other residents decreases, as shown by the decreasing difference between $R(a)$ and \bar{R} , in Figure 2. Second, the reproductive payoff of both resident strategies and, therefore, the mean resident payoff (\bar{R}) decreases be-

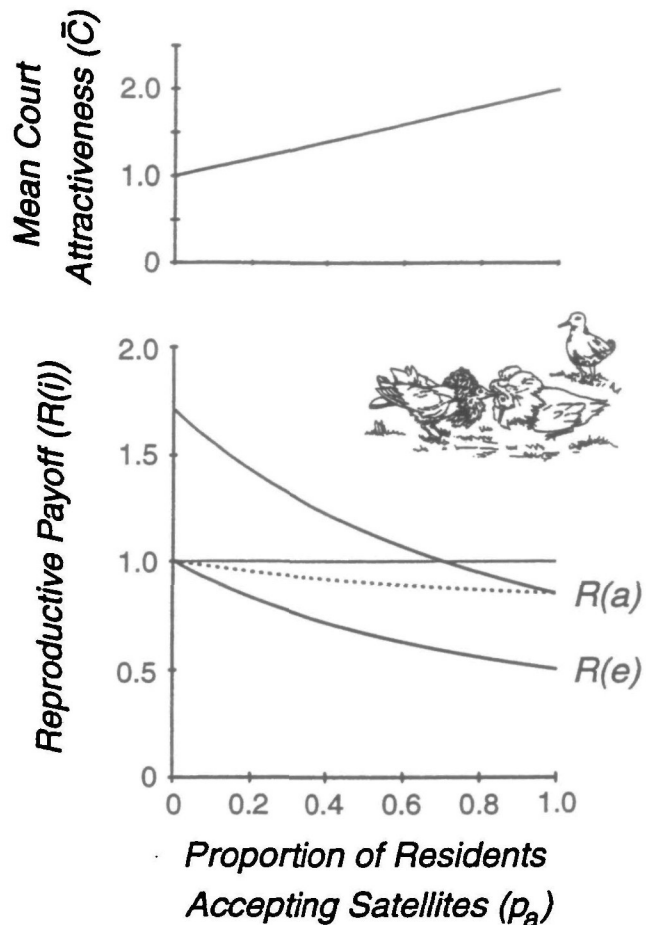


Figure 2
A graphical example of the resident's dilemma model given a constant proportion of satellites (P_s). The bottom panel shows the reproductive payoffs for accepting [$R(a)$] and excluding [$R(e)$] residents as a function of the proportion of the residents accepting satellites (p_a). The mean reproductive payoff of residents (\bar{R}) is indicated by the dashed line. The vertical axis of this panel is arbitrarily scaled such that the payoff to residents when all exclude satellites (i.e., $p_a = 0$) is 1, indicated by the grey horizontal line. The absolute scale of this axis will depend on the value of P_s . The top panel plots the mean court attractiveness (\bar{C}) in the population as a function of the proportion of the residents accepting satellites (p_a). See text for details of parameter values.

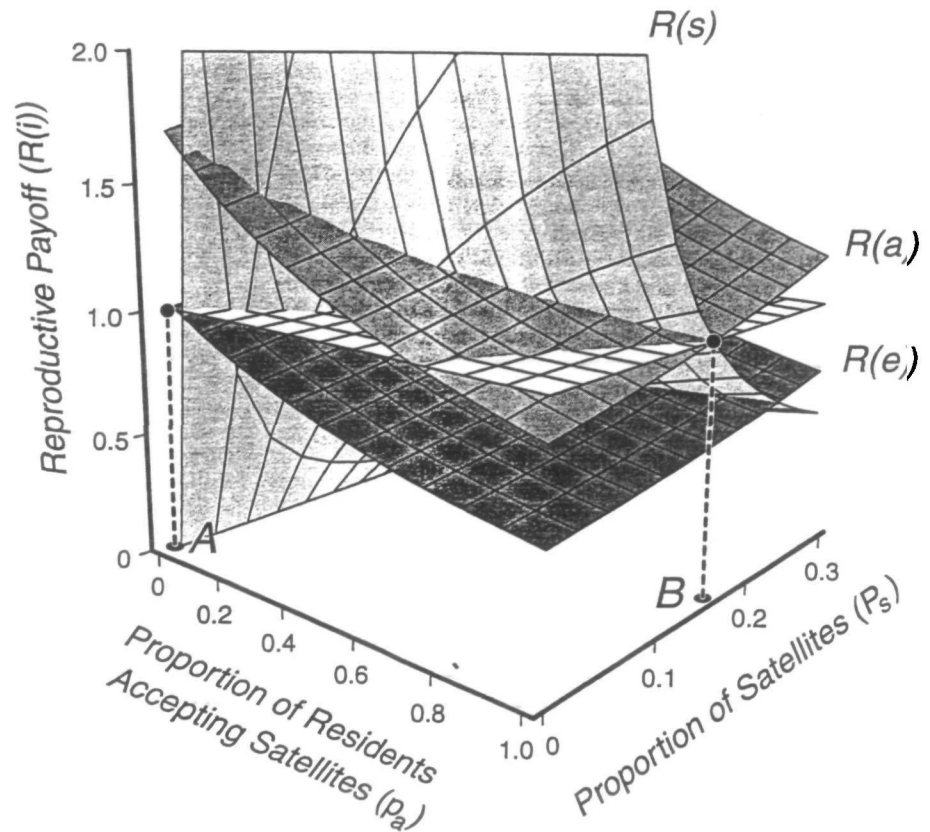
cause an increasing proportion of females are being mated by satellites. Despite this, the payoff to residents for accepting satellites [$R(a)$] continues to exceed the payoff for excluding them [$R(e)$], due to female preference for mating on co-occupied courts, leading to the eventual fixation of the accepting strategy among residents (i.e., $p_a = 1$). This equilibrium will be evolutionarily stable because accepting residents have a greater reproductive payoff than any mutant excluding resident that appears in the population. Figure 2 illustrates the resident's dilemma visually. Although all residents would benefit if satellites could be cooperatively excluded from leks, moving the population back to $p_a = 0$, any individual resident that defects and accepts satellites will receive a higher reproductive payoff.

Resident-satellite dynamics

So far, we have described the situation facing the residents given a constant proportion of satellites in the population.

Figure 3

A graphical example of the resident's dilemma model when the proportion of satellites (P_s) is free to evolve. The surfaces show the reproductive payoff to accepting [$R(a)$] and excluding [$R(e)$] residents and to satellites [$R(s)$] as a function of the proportion of residents accepting satellites (p_a) and the proportion of satellites in the population (P_s). The mean reproductive payoff of all breeding males, equal to the inverse of the breeding sex ratio ($1/S$), is indicated by the white, horizontal plane. Point A indicates the assumed "ancestral" population in which all breeding males are excluding residents. Point B is an evolutionarily stable equilibrium at which satellites exist at an equilibrium proportion (P_s), and all residents accept satellites onto their court. See text for details of parameter values.



Although P_s may currently be at equilibrium, it presumably has always been free to evolve. The evolution of P_s is frequency dependent. The greater the value of P_s , the smaller the payoff to satellites, because more of them compete for positions on fewer residents' courts (see Equation 2.3), and the greater the payoff to residents, because there are fewer courts (see Equation 1.0). We now show that when this second frequency-dependent dynamic is considered, the resident's dilemma need not result in a globally lower payoff to residents.

We evaluate the evolutionary dynamics of P_s assuming that the invasion condition is met and that all residents accept satellites. This simplification is possible because the invasion condition for satellite acceptance does not depend on the value of P_s . As per Taylor and Jonker (1978), we model the evolutionary dynamics of the satellite strategy, expressed as \dot{P}_s , the rate of change of P_s , as:

$$\dot{P}_s = P_s [R(s) - \bar{R}], \quad (4.0)$$

where \bar{R} is the mean reproductive payoff of males, which, since we assume that $p_a = 1$, is given by:

$$\bar{R} = P_s R(s) + (1 - P_s) R(a).$$

Setting Equation 4.0 equal to zero and solving for the equilibrium proportion of satellites, \hat{P}_s , produces the following:

$$\hat{P}_s = 1 - M_s. \quad (5.0)$$

The equilibrium proportion of satellites in the population will be equal to the proportion of court matings, which in our model is equivalent to the proportion of all matings they obtain. This equilibrium is evolutionarily stable if

$$\left. \frac{\partial \dot{P}_s}{\partial P_s} \right|_{\hat{P}_s} = -\frac{1}{S} < 0, \quad (6.0)$$

which is always true because S is positive.

We can now extend our previous example and explain why globally the resident's dilemma need not result in a lower reproductive payoff to residents. Figure 3 plots the reproductive payoffs for the accepting [$R(a)$] and excluding [$R(e)$] resident strategies and for the satellite strategy [$R(s)$] as a function of the proportion of residents accepting satellites (p_a) and the proportion of satellites in the male population (P_s). In Figure 2, we assumed a constant proportion of satellites corresponding to a vertical plane through Figure 3 at any value of P_s . Unlike in Figure 2, we now plot the mean reproductive payoff for all breeding males, \bar{R} (indicated by the white plane), rather than that of residents only (\bar{R}_r). \bar{R} is equal to the inverse of the breeding sex ratio ($1/S$) and is therefore constant with respect to p_a and P_s in this example.

In the ancestral lekking population, point A, all breeding males were excluding residents, each with the same expected reproductive payoff equal to $1/S$. Since the invasion condition for satellite acceptance is met, the accepting resident strategy will invade, assuming that some small proportion of males are willing to behave as satellites. As accepting invades, the payoff to satellites will quickly exceed the mean payoff (Figure 3), and their proportion in the population (P_s) will increase. Changes in P_s will not affect the invasion of satellite acceptance by residents, and eventually all residents will accept satellites. At the same time, frequency-dependent selection will equalize resident and satellite reproductive payoffs as the proportion of satellites in the population comes to equilibrium at a value equal to the proportion of matings they obtain (i.e., $\hat{P}_s = 1 - M_s$). At this new equilibrium, point B, all males, whether they are satellites or accepting residents, will again have the same expected share of breeding females and the same reproductive payoff equal to $1/S$. Thus, globally the failure of residents to cooperatively exclude satellites from leks

will not lower their payoffs as long as the breeding sex ratio remains constant.

It is plausible that the invasion of satellites and their acceptance by residents could enlarge the pool of breeding males and thereby increase the breeding sex ratio (S). In this case, the white surface of Figure 3, representing the mean payoff to breeding males ($\bar{R} = 1/S$) would slope downward between points A and B, and the resident's dilemma would result in globally lower payoffs to resident males. Regardless of whether this occurs, in a local sense residents males will always appear to face an evolutionary dilemma because, no matter what the value of P_r , the reproductive payoffs to residents will always experience the frequency dependence illustrated in Figure 2. Residents will always appear to benefit if satellites could be cooperatively excluded from courts. Again, however, the correct global interpretation requires consideration of the evolutionary dynamics of P_r . Even if residents could cooperatively exclude satellites from leks, this would only lead to satellite extinction and return the population to point A.

DISCUSSION

The resident's dilemma superficially resembles the prisoner's dilemma, the classic paradigm for the difficulties in achieving cooperation in a game-theoretical setting (Axelrod and Hamilton, 1981). The prisoner's dilemma has been used as an explanation for the communal breeding territories of the pukeko (*Porphyrio porphyrio*, Craig, 1984). However, the models differ in two important ways. First, the prisoner's dilemma is a two-player game, whereas the resident's dilemma is a game against the field and more realistically models the situation facing residents. More importantly, a noncooperative outcome in the resident's dilemma need not result in globally lower payoffs for residents, as it would in the prisoner's dilemma, due to frequency-dependent selection on the proportion of satellites in the population.

We modeled the benefit to residents for accepting satellites as increased court attractiveness to females without specifying the mechanisms behind the increase. For example co-occupied courts might be more attractive to females due to the combined attractiveness of the participating males through, for example, some runaway sexual selection mechanism. In this case, the outcome of the model would not depend on the relative attractiveness of residents and satellites. Alternatively, females might prefer co-occupied courts because resident-satellite interactions provide an opportunity to observe male characteristics relevant to female choice.

More generally, our model would apply to any relative benefit associated with accepting rather than excluding satellites from the court. Suppose, for example, that satellites functioned as personal predator sentinels for the resident. Residents that initially accepted satellites might enjoy a large reduction in predation risk relative to other residents. However, once sentinel acceptance fixes among residents, each resident might again be at the same risk to predators, thereby gaining nothing, yet each would pay the reproductive costs of accepting satellites.

Evolution and maintenance of satellites

We presented our model without considering how a satellite and accepting resident strategy could have invaded a population of excluding residents simultaneously. In particular, what success would pure satellite strategists have without the prior existence of sufficient numbers of accepting residents? The origin of the satellite behavior must have been more complicated than our simple model implies. Satellites could initially have been successful resident males that adopted satel-

lite behavior opportunistically with any other resident willing to accept them into transient reproductive coalitions for mutual benefit. Specialized satellite strategists could have evolved once acceptance became more widespread. Alternatively, satellites may have initially been less competitive, marginal males, with little or no expected breeding success that were willing to form coalitions with accepting residents as part of a conditional strategy to obtain some reproductive success (Lank and Smith, 1987). If this happened, the spread of satellite acceptance may have brought additional males into the breeding population, resulting in a higher breeding sex ratio and therefore a globally lower payoff to residents. However, once satellite acceptance was established among residents and the payoff to satellites exceeded that of residents, more competitive males would have been selected to take over the satellite role, thereby restoring the original breeding sex ratio.

Although our model suggests that resident-satellite associations are mutually beneficial, conflict nonetheless exists regarding the partitioning of court matings (i.e., the value of M_s). Residents appear to negotiate the value of M_s by controlling satellites directly, using aggressive behavior, while satellites threaten to disrupt matings or move to another court. In our model, we assume that M_s is constant, but residents and satellites might negotiate different values under different conditions (cf. van Rhijn, 1973). For example, satellites obtain the highest proportion of matings on leks of intermediate size (Hogan-Warburg, 1966, 1993; Höglund et al., 1993).

Our model shows how frequency-dependent selection could lead to an evolutionarily stable proportion of satellites in the male population. The model predicts that the equilibrium proportion of satellite (\hat{P}_s) will be equal to the proportion of matings they obtain ($1 - M_s$), assuming that independents and satellites have similar life histories. Estimates of the proportion of matings satellites obtain at leks average 15% ($n = 7$ studies with reasonable sample sizes, range: 7–28%: Brinkemper, 1979, personal communication; Hill, 1991; Hogan-Warburg, 1966; Höglund and Alatalo, 1995; Lank DB, Smith CM, unpublished data; van Rhijn, 1973, 1991). Estimates of \hat{P}_s are more problematic. It is difficult to estimate accurately the proportions of satellites by using data gathered at leks, since residents, satellites, and non-breeding "marginal" independents have different patterns of lek attendance (van Rhijn, 1973, 1991). Lek-based estimates of \hat{P}_s range between 13% and 34% (Hogan-Warburg, 1966; Höglund and Alatalo, 1995; van Rhijn, 1973, 1983, 1991). At the population level, Lank DB and Smith CM (unpublished data) found 16% satellites in systematic surveys at one site throughout two breeding seasons, and Jukema et al. (1995) estimated 10% satellites among birds caught and scored for plumage type on spring migration in Friesland. The broad similarity of the estimates for \hat{P}_s and $1 - M_s$ suggests agreement with the model's prediction, supporting the view that alternative male mating behaviors in ruffs represent evolutionarily stable alternative mating strategies.

Female choice for alternative male mating behavior

No previous model has considered a mechanism by which female mate choice directly favors the spread and maintenance of alternative male behaviors. General discussions have emphasized male-male interactions almost exclusively (e.g., Dawkins, 1980; Gadgil, 1972; Gross, 1984; Gross and Charnov, 1980; Rubenstein, 1980; Shuster, 1989; Waltz, 1982; Waltz and Wolf, 1984; but see Arak, 1984). This bias reflects the fact that, in most species, alternative male behaviors reflect conditional "best of a bad job" behavioral tactics by individuals that receive a lower payoff (Dawkins, 1980; Gross, 1996). Any association between males pursuing different tactics reflects par-

asitism of the more successful type. In such systems female choice may be irrelevant or, as demonstrated in a few studies, females may actually prefer one type of male over another (e.g., Howard, 1981; Ryan et al., 1990; Taboraky, 1994; van den Berghe et al., 1989), which would select against alternative male behaviors. In contrast, our analysis suggests that the resident-satellite relationship in ruffs, despite the obvious competitive elements, is fundamentally a cooperative association favored by female choice. This mutual benefit allows for the negotiation of equitable payoffs and the establishment of a stable equilibrium between alternative strategies.

Our model might seem to apply to long-tailed manakins (*Chiroxiphia linearis*), the premiere example of close cooperation between unrelated males in a breeding arena (McDonald and Potts, 1994). However, this system differs from ruffs in that there are no alternative strategies. Subordinate males are not competing with the current alpha male to mate with females but instead are cooperating with him to gain inheritance rights to the display site. Thus, this system represents cooperation, presumably due to female choice, but between tactics within a single conditional strategy rather than between alternative strategies.

A more plausible parallel situation may be found in species of fish with male satellites at spawning sites (Taboraky, 1994), including bluegill sunfish (*Lepomis macrochirus*). Nesting male sunfish court smaller males that mimic females, just as they do real females (Dominey, 1981). This has usually been interpreted as a failure of nesting males to discriminate between mimics and real females (Gross, 1982). Alternatively, mimics might be discriminated, but nonetheless recruited by nesting males, if females prefer to spawn at locations chosen by other females at rates sufficient to offset the loss of a portion of the fertilizations obtained (Dominey, 1981). The process assumes that females would be fooled but does not require that nesting males, which are in closer contact with the female mimics, would be unable to discriminate between the sexes. The evolutionary dynamics would be similar to those modeled here and, as in ruffs, we would expect nesting males actively to court their rivals, as observed. Additional fish species that might be examined for similar behavior are reviewed in Taboraky (1994).

Our analysis supports the view that female preference for mating within male associations is responsible for the evolution of the alternative male mating strategies in ruffs. It seems parsimonious to assume that female choice is also responsible for the evolution of male association to form leks in this species. Indeed, both observational and experimental studies directly support the role of female choice in maintaining lekking in ruffs (Höglund et al., 1993; Lank and Smith, 1992), although more parasitic hotshot-like processes also affect lek size (Widemo and Owens, 1995). The mating system of ruffs may be viewed as a complicated web of successful and failed cooperation driven by female preference for mating within male associations. Residents cooperate to form leks in order to attract females. Within leks, satellites and residents cooperate to form transient "leks within leks" for the same reason and because cooperation among residents to prevent such coalitions is unstable.

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REFERENCES

- Andersson M, 1994. Sexual selection. Princeton, New Jersey: Princeton University Press.
- Arak A, 1983. Male-male competition and mate choice in anuran amphibians. In: Mate choice (Bateson P, ed). Cambridge: Cambridge University Press; 181-210.
- Arak A, 1984. Sneaky breeders. In: Producers and scroungers (Barnard, CJ, ed). London: Croom Helm; 154-194.
- Austad SN, 1984. A classification of alternative reproductive behaviors and methods for field-testing ESS models. *Am Zool* 24:309-320.
- Axelrod R, Hamilton WD, 1981. The evolution of cooperation. *Science* 211:1590-1596.
- Balmford A, Deutsch JC, Nefdt RJC, Clutton-Brock T, 1993. Testing hotpot models of lek evolution: data from three species of ungulates. *Behav Ecol Sociobiol* 33:57-65.
- Beehler BM, Foster MS, 1988. Hotshots, hotspots, and female preferences in the organization of lek mating systems. *Am Nat* 131:203-219.
- Bradbury JW, 1981. The evolution of leks. In: Natural selection and social behavior (Alexander RD, Tinkle D, eds). New York: Chiron Press; 138-169.
- Bradbury JW, Gibson RM, 1983. Leks and mate choice. In: Mate choice (Bateson P, ed). Cambridge: Cambridge University Press; 109-138.
- Brinkkemper J, 1979. De Kempphaan in Nederland. Wetenschappelijke mededelingen Koninklijke Nederlandse Natuurhistorische Vereniging 137. Amsterdam: ERLA.
- Caro TM, Bateson P, 1986. Organization and ontogeny of alternative tactics. *Anim Behav* 34:1483-1499.
- Clutton-Brock TH, Deutsch JC, Nefdt RJC, 1993. The evolution of ungulate leks. *Anim Behav* 46:1121-1138.
- Clutton-Brock TH, Price O, MacColl A, 1992. Mate retention, harassment and the evolution of ungulate leks. *Behav Ecol* 3:234-242.
- Craig JL, 1984. Are communal pukeko caught in the prisoner's dilemma? *Behav Ecol Sociobiol* 14:147-150.
- Cramp S, Simmons KEL (eds), 1983. The birds of the western Palearctic, vol. 3. Oxford: Oxford University Press.
- Dawkins R, 1980. Good strategy or evolutionarily stable strategy? In: Sociobiology: beyond nature/nurture (Barlow GW, Silverberg J, eds). Boulder, Colorado: Westview Press; 331-367.
- Dominey WJ, 1981. Maintenance of female mimicry as a reproductive strategy in bluegill sunfish (*Lepomis macrochirus*). *Environ Biol Fish* 6:59-64.
- Gadgil M, 1972. Male dimorphism as a consequence of sexual selection. *Am Nat* 119:574-580.
- Gibson RM, Taylor CE, Jefferson DR, 1990. Lek formation by female choice: a simulation study. *Behav Ecol* 1:36-42.
- Goaling LM, 1986. The evolution of mating strategies in male antelope. In: Ecological aspects of social evolution: birds and mammals (Rubenstein DI, Wrangham RW, eds). Princeton, New Jersey: Princeton University Press, 244-281.
- Gross MR, 1982. Sneakers, satellites and parentals: polymorphic mating strategies in North American sunfishes. *Z. Tierpsychol* 60:1-26.
- Gross MR, 1984. Sunfish, salmon and the evolution of alternative reproductive strategies and tactics in fishes. In: Fish reproduction: strategies and tactics (Potts G, Wootton R, eds). London: Academic; 55-75.
- Gross MR, 1996. Alternative reproductive strategies and tactics: diversity within sexes. *Trends Ecol Evol* 11:92-98.
- Gross MR, Charnov EL, 1980. Alternative male life histories in bluegill sunfish. *Proc Natl Acad Sci USA* 77:6937-6940.
- Grosskopf G, 1968. Die Vögel de Insel Wangerooge. Jever: C.L. Metzcker and Söhne.
- Hill WL, 1991. Correlates of male mating success in the ruff *Philomachus pugnax*, a lekking shorebird. *Behav Ecol Sociobiol* 29:367-372.
- Hogan-Warburg AL, 1966. Social behaviour of the ruff, *Philomachus pugnax* (L.). *Ardea* 54:109-229.
- Hogan-Warburg AL, 1993. Female choice and the evolution of mating strategies in the ruff *Philomachus pugnax* (L.). *Ardea* 80:395-403.
- Höglund J, Alatalo R, 1995. Leks. Princeton, New Jersey: Princeton University Press.
- Höglund J, Robertson JGM, 1990. Female preferences, male decision

- rules, and the evolution of leks in the great snipe *Gallinago media*. *Anim Behav* 40:15–22.
- Högland J, Montgomerie R, Widemo F, 1993. Costs and consequences of variation in the size of ruff leks. *Behav Ecol Sociobiol* 32:31–39.
- Howard RD, 1981. Male age-size distribution and male mating success in bullfrogs. In: Natural selection and social behavior (Alexander RD, Tinkle DW, eds). New York: Chiron Press; 61–77.
- Howard RD, 1984. Alternative mating behaviors of young male bullfrogs. *Am Zool* 24:397–406.
- Jukema J, Pierama T, Louwsma L, Monkel C, Rijpma U, Visser K, van der Zee D, 1995. Rui en gewichtsveranderingen van doortrekkende Kemphanen in Friesland in March-April 1993 en 1994. *Vanellus* 48: 55–61.
- Lack, D, 1968. *Ecological adaptations for breeding in birds*. London: Chapman and Hall.
- Lank DB, Smith CM, 1987. Conditional lekking in ruff (*Philomachus pugnax*). *Behav Ecol Sociobiol* 20:137–145.
- Lank DB, Smith CM, 1992. Females prefer larger leks: field experiments with ruffs (*Philomachus pugnax*). *Behav Ecol Sociobiol* 30: 323–329.
- Lank DB, Smith CM, Hanotte O, Burke TA, Cooke F, 1995. Genetic polymorphism for alternative mating behaviour in lekking male ruff, *Philomachus pugnax*. *Nature* 378:59–62.
- Männikkö E, 1989. Suo kutsuu suokukkoja turnajaisiin. *Eläinmaailma* 5:26–33.
- Maynard Smith J, 1982. *Evolution and the theory of games*. Cambridge: Cambridge University Press.
- McDonald DB, Potts WK, 1994. Cooperative display and relatedness among males in a lek-mating bird. *Science* 266:1030–1032.
- Phillips JB, 1990. Lek behaviour in birds: do displaying males reduce nest predation? *Anim Behav* 39:555–565.
- Queller DC, 1987. The evolution of leks through female choice. *Anim Behav* 35:1424–1432.
- Rubenstein DJ, 1980. On the evolution of alternative mating strategies. In: Limits to action: allocation of individual behavior (JER Staddon, ed). New York: Academic Press; 65–100.
- Ryan MJ, Hews DK, Wagner WE Jr, 1990. Sexual selection on alleles that determine body size in the swordtail *Xiphophorus nigrensis*. *Behav Ecol Sociobiol* 26:231–237.
- Scheuffler H, Stiefel A, 1985. Der Kampfäufer. Wittenberg: Ziemsen.
- Shepard JM, 1975. Factors influencing female choice in the lek mating system of the ruff. *Living Bird* 14:87–111.
- Shuster SM, 1989. Male alternative reproductive strategies in a marine isopod crustacean (*Paracerasis sculpia*): the use of genetic markers to measure differences in fertilization success among α -, β -, and γ -males. *Evolution* 43:1683–1698.
- Taborsky M, 1994. Sneakers, satellites, and helpers: parasitic and cooperative behavior in fish reproduction. *Adv Studies Behav* 23:1–100.
- Taylor PD, Jonker LB, 1978. Evolutionary stable strategies and game dynamics. *Math Biosci* 40:145–156.
- van den Berghe EP, Wernerus F, Warner RR, 1989. Female choice and the mating cost of peripheral males. *Anim Behav* 38:875–884.
- van Rhijn JG, 1973. Behavioural dimorphism in male ruffs, *Philomachus pugnax* (L.). *Behaviour* 47:153–229.
- van Rhijn JG, 1983. On the maintenance of alternative strategies in the ruff *Philomachus pugnax*. *Ibis* 125:482–498.
- van Rhijn JG, 1991. *The ruff*. London: Poyser.
- Waltz EC, 1982. Alternative mating tactics and the law of diminishing returns: the satellite threshold model. *Behav Ecol Sociobiol* 10:75–83.
- Waltz EC, Wolf LL, 1984. By jove!! Why do alternative mating tactics assume so many different forms? *Am Zool* 24:333–343.
- Westcott DA, 1994. Leks of leks: a role for hotspots in lek evolution? *Proc R Soc Lond B* 258:281–286.
- Widemo F, Owens IPF, 1995. Lek size, male mating skew and the evolution of lekking. *Nature* 373:148–151.
- Wiley RH, 1991. Lekking in birds and mammals: behavioral and evolutionary issues. *Adv Studies Behav* 20:201–291.
- Wittenberger JF, 1978. The evolution of mating systems of grouse. *Condor* 80:126–137.
- Wrangham RD, 1981. Female choice of least costly males: a possible factor in the evolution of leks. *Z Tierpsychol* 54:357–367.