

On the maintenance and origin of alternative strategies in the Ruff *Philomachus pugnax*

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This paper has tried to answer the question of how the independent and the satellite strategy of the Ruff originated and has been maintained during evolution. It is not intended as a report of a piece of completed research but gives a number of tentative, but testable hypotheses.

Data are presented that independent males and satellites are equally successful in copulating, provided that almost all copulations occur on leks, and independent males and satellites spend an equal proportion of their time on leks. The extent that males with the different strategies are attached to leks is analysed. Within the group of independent males, considerable differences exist: a resident male is strongly attached to only one particular lek and a marginal male seems to sample many leks. A satellite male behaves intermediately: he is attached to a limited number of leks. The mechanism for the maintenance of both strategies could not be explained by competition for resources (copulations). Contests between independent males and satellites are asymmetric, the satellite being the weaker contestant. The mechanism seems to be due to enlarging the accessibility of the resource by cooperation between both strategies.

The ideas on the origin of the system are based mainly on the behaviour of females. There is no relation between the distribution of leks and the size of a female's foraging area, except that most leks are situated along the migration route. It further seems that the number of copulating females in the Netherlands is larger than the number of males on leks, but the number of breeding females is much lower. It is suggested that many females copulate on migration, which is related to extreme breeding conditions in the north of the range. Apart from a change in the sex ratio from south to north, a change in the proportion of satellites is also predicted. The origin of the system is ascribed to the incompatibility between favourable food conditions for chicks and further possibilities for inter-male competition on leks in the same area. The satellite strategy is considered as being derived from a non-competitive strategy accompanying females on migration. In the phase of cooperation between resident and satellite males, individual recognition became important. This could be the factor underlying the evolution of white plumages in satellites and the extreme plumage diversity in independent males.

Courtship and mating of the Ruff *Philomachus pugnax* normally occurs on leks (Hogan-Warburg 1966, van Rhijn 1973). In these communities two groups of males, independent and satellite, can be distinguished. This classification is based upon differences in territoriality and in behaviour. Independent males are the potential owners of territories on a lek; their behaviour repertoire includes a variety of fighting and threat activities. Satellite males normally do not defend territories; their behaviour rarely involves threat activities and only in exceptional cases do they fight. Independent males can be further subdivided into resident males and marginal males. Residents are the actual owners of territories (residences). A marginal male on a lek does not possess a residence there but may have one on another lek. His behaviour may contain elements aimed at the acquisition of a residence. The status of a resident may be interchanged with that of a marginal male. Residents may lose their residences, and marginal males are the potential possessors. A satellite male exploits the residences of the territory owners. A visiting satellite is, in contrast to neighbouring resident males or marginal males, often tolerated by a resident, especially when no females are present.

This classification of independent and satellite males is highly correlated with differences in nuptial plumages: independent males have predominantly dark

coloured ruffs and head-tufts, satellite males in general are white. Both field and cage observations of the same individuals during successive years revealed that plumage and status are fairly constant. During his first spring, a male's ruff and head-tufts are relatively small and contain colour characteristics of the winter plumage. During later seasons these winter characteristics may completely disappear and the remaining more brilliant colours recur year after year. Similarly the status of a male is not very clear during his first season. Characteristics of both independent and satellite behaviour may be observed, but after the establishment of status in the second season, changes have only been observed under extreme conditions.

This constancy in both plumage and status suggests that behavioural differences are connected with genetical variants. Breeding experiments in our laboratory have not been very successful. The only two males with known fathers, which were reared until plumage colour and status were specified, did not obviate this hypothesis.

Hogan-Warburg (1966) suggested that genes for status and plumage were closely linked. Van Rhijn (1973) reasoned that status and plumage could be affected by the same genes with pleiotropic effects. This was based on the fact that certain plumage types exclusively occur in independent males (any ruff and black-tufts: independent plumages), others exclusively in satellites (white ruff and head-tufts, at least one without any pattern: satellite plumages), and that only part of the possible combinations (atypical plumages) occur in both categories of males. The most parsimonious hypothesis which could be deduced from these facts is that one locus with two alternative alleles is responsible for status and certain plumage characteristics: one homozygous combination resulting in independent males with independent plumages, the other homozygous combination resulting in satellite males with satellite plumages, and the heterozygous combination resulting in atypical plumages. This hypothesis could not be rejected by applying Hardy-Weinberg's law on the frequencies of males with different plumage types on four leks in the Netherlands. Van Rhijn (1973) suggested that, within the group with atypical plumages, external factors influence which status a juvenile male will adopt: if independent plumages are rare, males with atypical plumages are inclined to adopt the independent status; if satellite plumages are rare, they preferentially adopt the satellite status.

In certain cases the existence of alternative strategies in a species has been conceived as a 'mixed evolutionary stable strategy' or ESS (Parker 1978, Brockman, Grafen & Dawkins, 1979, Maynard Smith 1979). This implies that the reproductive success resulting from a strategy depends on the frequencies with which the other strategies are used in a population, and further that at equilibrium the successes of the different strategies should be equal (Bishop & Cannings 1978). The behaviour of the Ruff has been considered as a possible example of a 'mixed ESS' among higher vertebrates (Maynard Smith 1979).

This paper is intended to develop a theory about the evolution of the Ruff, and hence to offer a framework for future research on this species. Old and new data will be brought together in order to indicate by which selective forces the peculiar mating system of the Ruff could be maintained, and by which factors it could have originated during evolution. The extent to which the concept of a 'mixed ESS' is useful for such an approach will be discussed.

MAINTENANCE OF BOTH STRATEGIES

Assume that the frequencies of the two strategies are in equilibrium. Then, the average reproductive success of an independent male has to be equal to that of a satellite male. The only data related to reproductive success refer to copulation

frequencies on leks. Since females may copulate on different leks with several males for one clutch of eggs, it is not known whether the number of copulations of a male is linearly related to his number of descendants. Such a linear relationship, however, is plausible, and for lack of better information I will assume that it exists. If it is further assumed that the great majority of copulations occur on leks, then, the average copulation frequency of an independent male on leks should equal the average copulation frequency of a satellite male on leks.

The differences between the percentages of copulations performed by satellite males in three sets of observations (Table 1) are not very large. There are considerable differences between the proportions of satellite males in five sets of observations. A further inspection of the data shows that in set A the percentage of copulations by satellites strongly differs from the proportion of satellites. On the other hand in set B the percentage of copulations by satellites is equal to the proportion of satellites in the population. Thus, set B supports the hypothesis that the average copulation frequencies of a satellite and an independent male are similar, but set A is incompatible with this hypothesis.

How can these contradictions be explained? There are two possibilities: first, the initial assumptions are invalid, and secondly, the estimates for copulation frequency and/or frequency of occurrence of satellites are wrong.

It could be suggested that the system is not at equilibrium and that the agreement in set B arose by chance, or was an artefact of the way of measuring satellite proportion. The only support for the equilibrium assumption can be gathered from the literature. The satellite-independent system in the Ruff seems to be a general phenomenon, both in time and space (Selous 1906-07, Turner 1920, Bancke & Meesenburg 1952, 1958, Spillner 1971, Shepard 1975). Evidence for changes in satellite proportions is not available.

The assumption that the number of copulations of a male is linearly related to his number of descendants seems to be very plausible for each male category; however, among the various categories this relationship might be different. It has been shown by van Rhijn (1973) that copulations by satellite males mainly occur at the beginning of the season. In view of the laying dates of the females it is conceivable that these early copulations result in more offspring than later ones; in other words, on average

TABLE 1

Percentage of copulations (C) by satellite male Ruff and satellite proportion (P) in different sets of observations

C	P	Material	Source
11		Out of 496 copulations ¹ by the males on seven leks in five different areas	All own observations 1968-72
18	34% (A)	Out of 132 copulations ¹ and 95 males visiting four leks in two different areas	Hogan-Warburg (1966) table 14
13	13% (B)	Out of 219 copulations ¹ and altogether 1590.5 h spent by males on six leks in five different areas	Own observations 1969-71
	35%	Out of 309 males visiting ten leks in four different areas	Hogan-Warburg (1966) table 11
	7% ²	Out of 460 males in two large foraging flocks in the north of the Netherlands	Own observations 21 April 1969
	4% ²	Out of 233 males in 26 flying groups in the north of the Netherlands	Own observations April and May 1979

Note: ¹Number of Reeves involved unknown, but at least 25% of the number of copulations.

²Data refer to males with white head-feathers.

a satellite copulation may be more successful than a copulation by an independent male. On the other hand, satellite copulations seem to be more often disturbed by other males than copulations by independent males. Although all clear cases of interferences were not taken into account in the final copulation score, the proportion of undetected interferences (unsuccessful copulations) in the satellite copulation score could be higher than in the score for independent males.

The assumption that the great majority of the copulations occur on leks is based on the fact that almost all copulations of Ruffs have been observed there. The number of observation hours on leks, however, greatly exceeds the time spent in observing temporarily displaying groups of Ruffs. Nevertheless, these groups without site-attachment frequently occur and seem to include a considerable proportion of satellite males. These groups are far less stable than leks. Van Rhijn (1973) argued that instability raises the chances for satellite males. If copulations were no rare events in these temporary groups, it is conceivable that satellite males are able to compensate for—perhaps—low success on leks.

The second point which has to be considered refers to the accuracy with which copulation frequency and frequency of occurrence of satellites could be estimated. I am fairly confident about the copulation frequencies on leks; they refer to several hundred hours of observation and it is unlikely that mistakes have been made in the identification of the status of the copulating male. Furthermore, the differences between the percentages in Table 1 are not large. The estimate of the frequency of occurrence of satellites is far less reliable: proportions are quite different. Satellite males (and marginal males) may visit several leks. By counting the number of satellites on a particular lek (as Hogan-Warburg did), one may get an impression of the number of satellites in a certain area. In contrast to this, a resident male is strongly attached to only one particular lek. It is therefore likely that, if the number of independent males is not strongly affected by marginal males, the proportion of satellites observed on a particular lek is higher than the proportion of satellites in the population. Thus, the proportion of satellites as estimated by Hogan-Warburg (e.g., data set A) seems to be too high.

To obtain a reliable measure for the proportion of satellites in the population, I used two other methods by which it was possible to get around the difficulty of satellite and marginal males visiting different leks. The first method refers to observations of flying and foraging Ruffs in the field, the second to the time spent on leks by the different categories of males.

The proportion of males with white head-feathers in groups of flying and foraging Ruffs (Table 1) was considerably lower than the estimates based on Hogan-Warburg's data. I suspect that this is a reasonable measure, since most satellite males have white ruffs and head-tufts (even in winter satellite males may often be distinguished by their white heads) and only a small proportion of the independent males possesses white head-feathers. Nevertheless the proportions obtained by this method were also lower than the percentage of copulations performed by satellites. It could be possible, however, that satellites were under-represented, because they did not tend to associate with the kind of groups I was able to check.

The second method of obtaining a reliable measure of the proportion of satellites was based on the assumption that all males spend an equal proportion of their time on leks. Then the proportion of satellites in a population is given by the sum of the duration of satellite visits to leks divided by the sum of the duration of all male visits to leks. It is remarkable that the proportion given in set B equals the percentage of copulations performed by satellites during the same period. To test the validity of this proportion of 13% satellites in the population, the underlying assumption (all males spend an equal proportion of their time on leks) has to be further investigated.

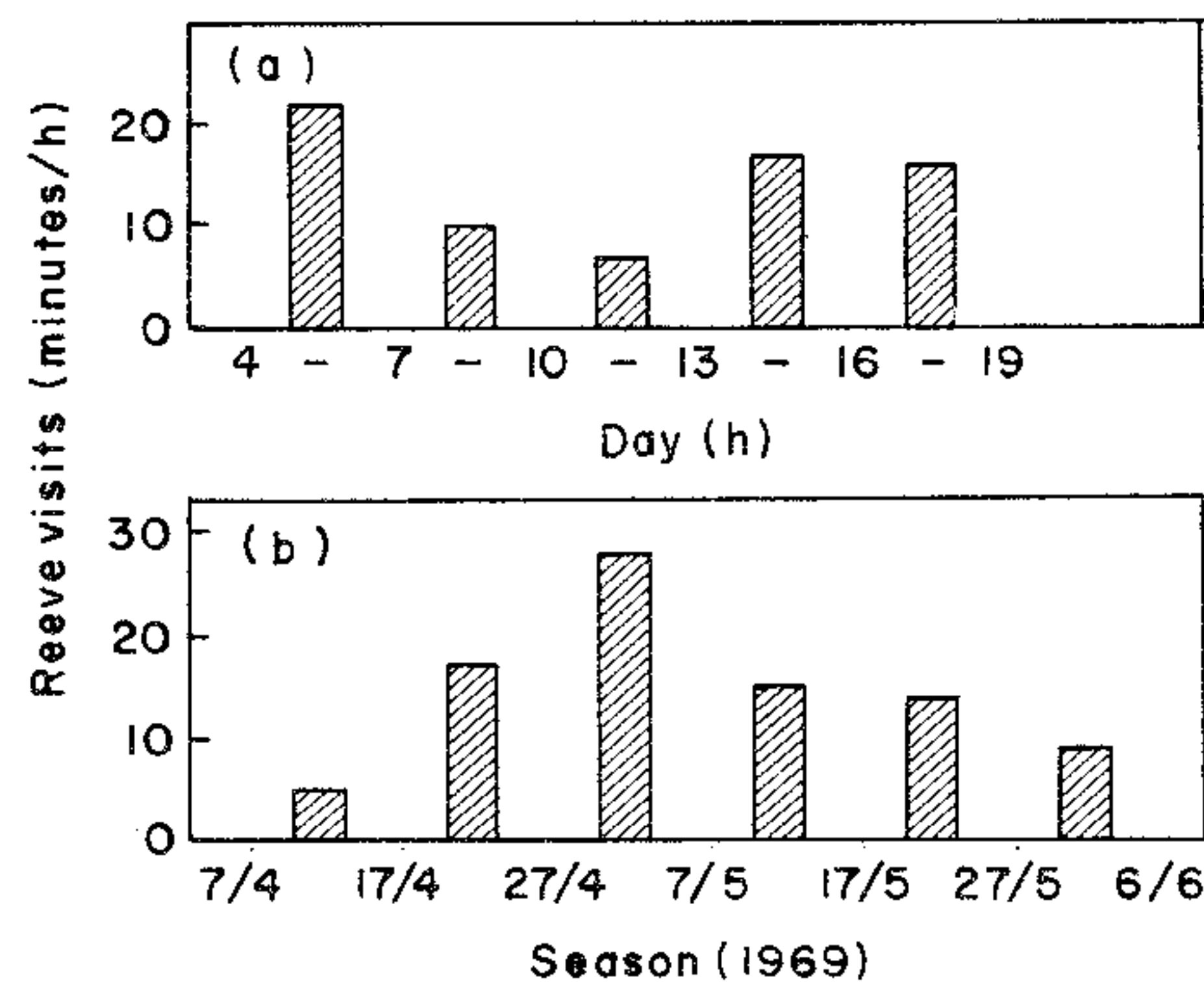


FIGURE 1. Sum of the durations of Reeve visits to a lek (minutes/h) at different times of the day (a) and the season (b).

ATTACHMENT TO LEKS

It is likely that the main selection pressure acting on males to visit leks is to increase their chances of copulating. Hence, one should expect that males select those periods for visiting leks when females (potential copulation partners) may land and stay for some time. Figure 1 shows, for one season at one lek, how female visits are related to time of day and season. Females may visit a lek at any time of the day, but the probability of female visits varies to some extent with time.

If almost all copulations occurred on leks, a male should spend as much time there as possible, and select the periods with the highest probability of female visits. Figure 2 demonstrates how long different individual males and different categories of individuals were present on one lek during two observation sessions on consecutive days. On both days the three individually recognizable satellites and the five marginal males spent less time on this lek than the seven resident males (all cases: $P < 0.05$, two tailed, Mann-Whitney U test). On both days the durations that one or more satellites were present, or that one or more marginal males were present (hatched columns), were even smaller than each of the seven durations for individual resident males. Further it seems that on days with long durations of female presence (30 April) males tended to spend more time on the lek than on days when females were there only briefly (1 May). For the seven resident males the difference between the two observation sessions was statistically significant ($P < 0.05$, two tailed, Wilcoxon matched-pairs signed-ranks test).

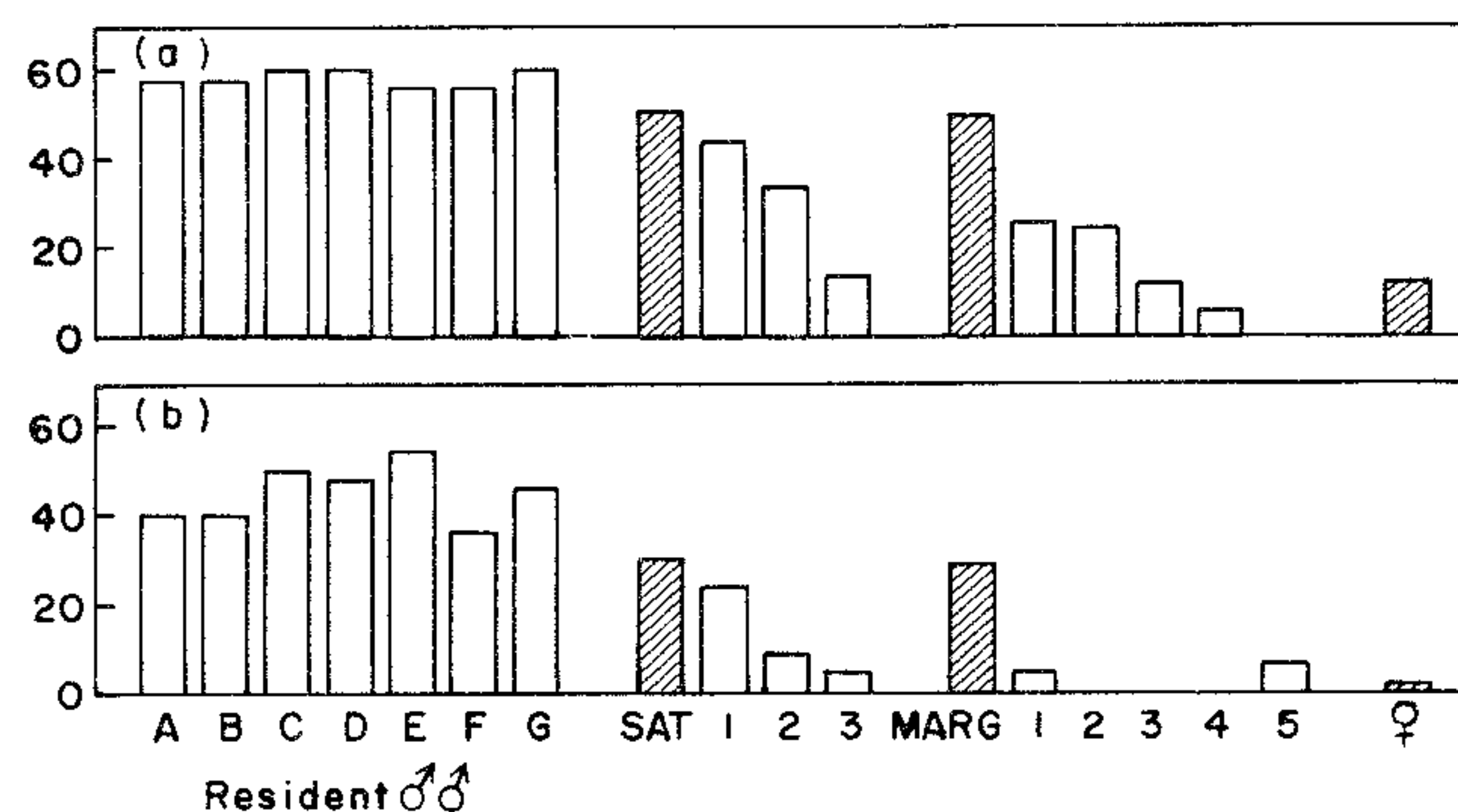


FIGURE 2. Number of minutes/h spent on the lek by seven resident male Ruff, three satellites, and five marginal males on two consecutive days. (a) 30 April and (b) 1 May 1969. Hatched columns refer to number of minutes/h with at least one satellite, one marginal male, or one Reeve present.

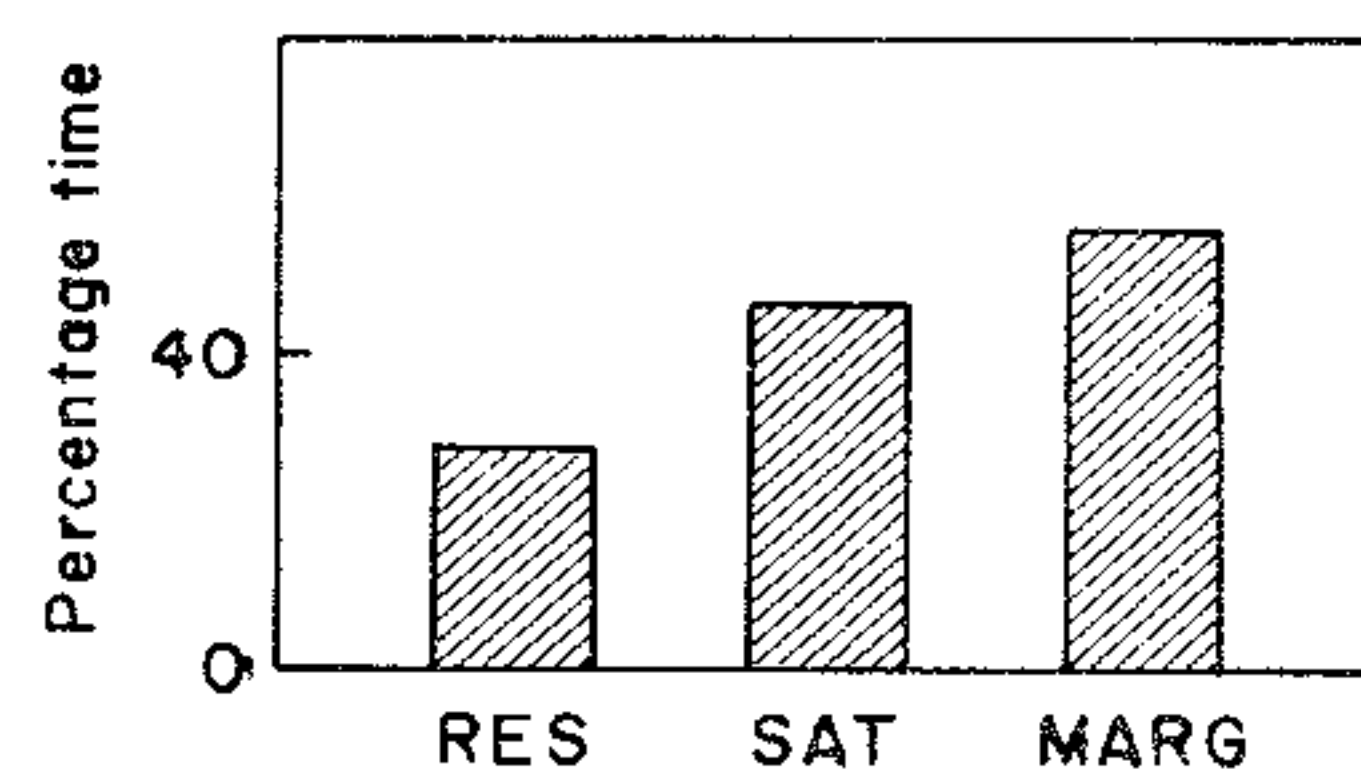


FIGURE 3. Average percentage of time of a resident male Ruff ($n \geq 190$), a satellite ($n \geq 70$), and a marginal male ($n \geq 115$) spent together with at least one Reeve on the lek.

The finding that a resident male spends more time on a particular lek than each satellite or marginal male is probably related to territory defence. I observed several times that resident males, spending less time on the lek than their companions, lost their territories to intruding marginal males or were forced to exchange their better quality territory for a worse one. This may preclude them from visiting different leks. Normally they only leave the lek for short communal foraging trips in the close vicinity. On the other hand, I observed satellite and marginal males visiting different leks depending on the presence of females. Particularly at the beginning of the season, females visit leks in flocks and quite often fly from one lek to another. Female visits to different leks in the same area are not necessarily synchronized. If experience on a particular lek is not very important for satellite and marginal males, it should be a good strategy to search for leks with many females and to leave leks without females. One might therefore expect that satellite and marginal males spend more time together with females on leks than resident males. This expectation is confirmed by data (Fig. 3) based on 191 h observation on six leks in five different areas in the Netherlands (1969–71). Marginal males spend even more time with females than satellite males do.

An analysis of the conditions under which individuals of the different categories arrived on or departed from one of the leks observed during 83 h from 17 April to 5 June 1969 also confirmed this strategy. Satellite and marginal males arrived/departed more often than resident males when females were present on the lek (Fig. 4). Both satellite and marginal males arrived more often when females were already present than they departed when females were staying on the lek. Finally, marginal males selected higher densities of females than satellite males: they tended to arrive/depart more often than satellite males when females were present on the lek (all cases: $P < 0.05$, two tailed, Chi-square test, 1 df).

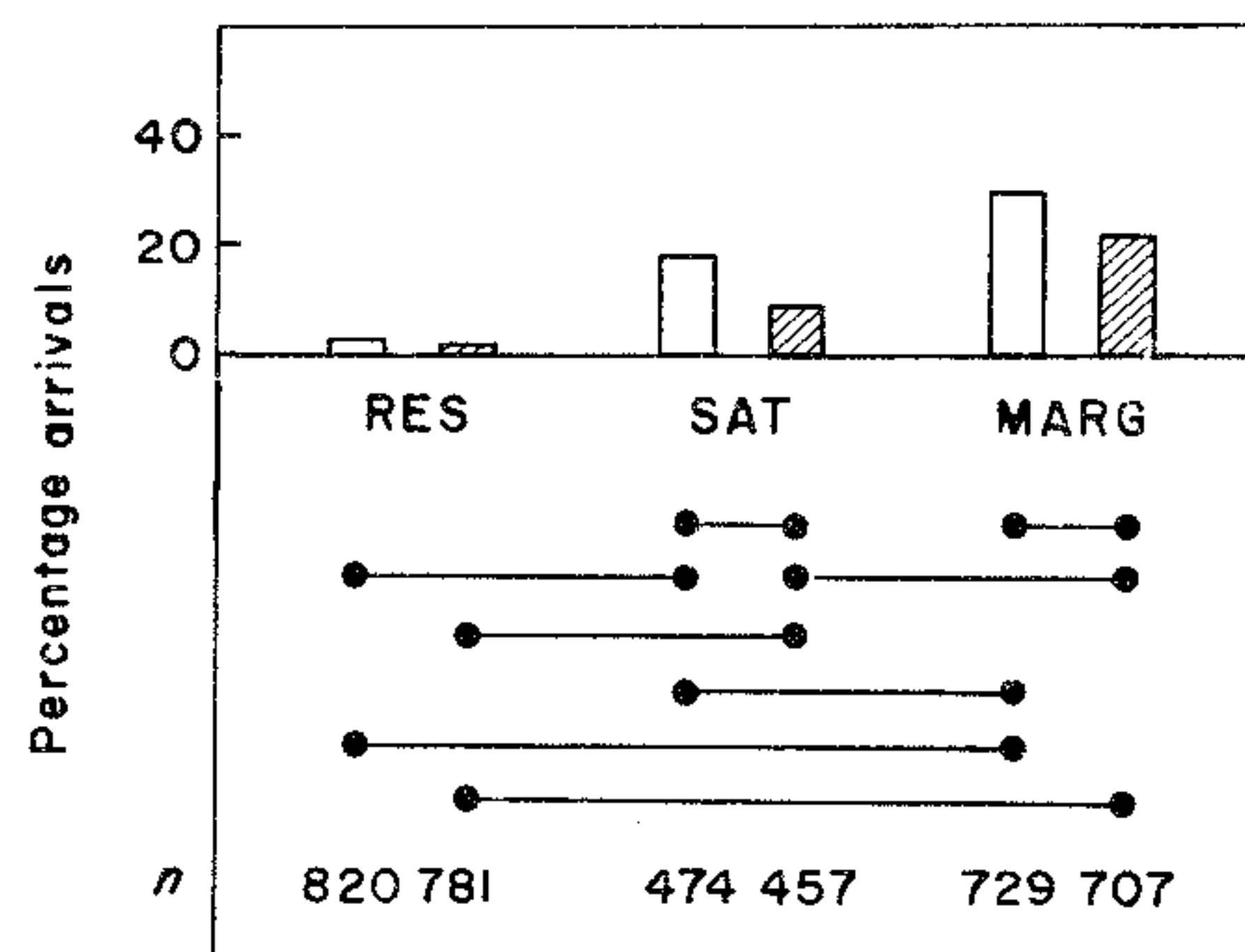


FIGURE 4. Percentage of arrivals ($\square$) and departures (hatched) by 11 resident male Ruff, at least six satellites, and at least 14 marginal males, when Reeves were already present (arrival) or stayed (departure) on the lek. Horizontal lines indicate significant differences ($P < 0.05$).

Figure 5 (based on the same observations as Fig. 4) suggests that satellite and marginal males succeeded in finding leks with many females by associating with flying females: they more often than resident males arrived on or departed from leks together with females (all cases: $P < 0.05$, two tailed, Chi-square test, 1 df).

To summarize these data: a resident male is strongly attached to one particular lek, a satellite male prefers periods when there are females visiting, and a marginal male also strongly prefers those periods. Both individual satellite and marginal males have been found to visit different leks in the same area during the same season and even on the same day. It might thus be possible that they spend almost all their time on leks and fly from one lek to another depending on the presence of females. The finding that satellite males have a less pronounced preference for periods when females visit than marginal males may be associated with a stronger attachment to certain leks. A considerable proportion of the satellites in a certain area can be observed during the whole season, while individual marginal males can mostly be tracked for only a few days. Furthermore, many satellites spend most of their time with their own preferred resident males on the different leks. It is therefore plausible that reproductive success of satellites is positively influenced by experience on the leks they visit.

I suggest that the selection pressure acting on marginal males to visit leks is not primarily copulation, but to acquire a territory to open the possibility of reproduction. This supposition is supported by the fact that I never saw marginal males copulating on or near leks. It may be possible that marginal males, before investing much energy in settling a territory, explore female visiting rates on different leks in order to find the best solution for future reproductive success. The marked preference of marginal males for periods when females visit may also be associated with better chances for settling a territory. To investigate this suggestion I calculated the extent to which individual males of the different categories were subject to attacks by resident males during the absence or presence of females. The results, comprising 83 h observation on one lek (1969), are shown in Figure 6. Both resident and satellite males are, in the majority of the cases, significantly more often attacked by resident males in the presence of females than during their absence (Chi-square test, two tailed, 1 df). Marginal males, however, do not seem to suffer more from attacking resident males during female presence. It is conceivable that males are strongly inclined to resist attacks when females are nearby. Hence, for marginal males, female presence is a favourable condition for settling territories. In fact almost all territory establishments and exchanges have been observed during high visiting rates of females.

The tendency of males of the different categories to associate with foraging females and to build up temporarily displaying groups certainly interferes with their attachment to leks. Nevertheless these groups can be observed frequently, which

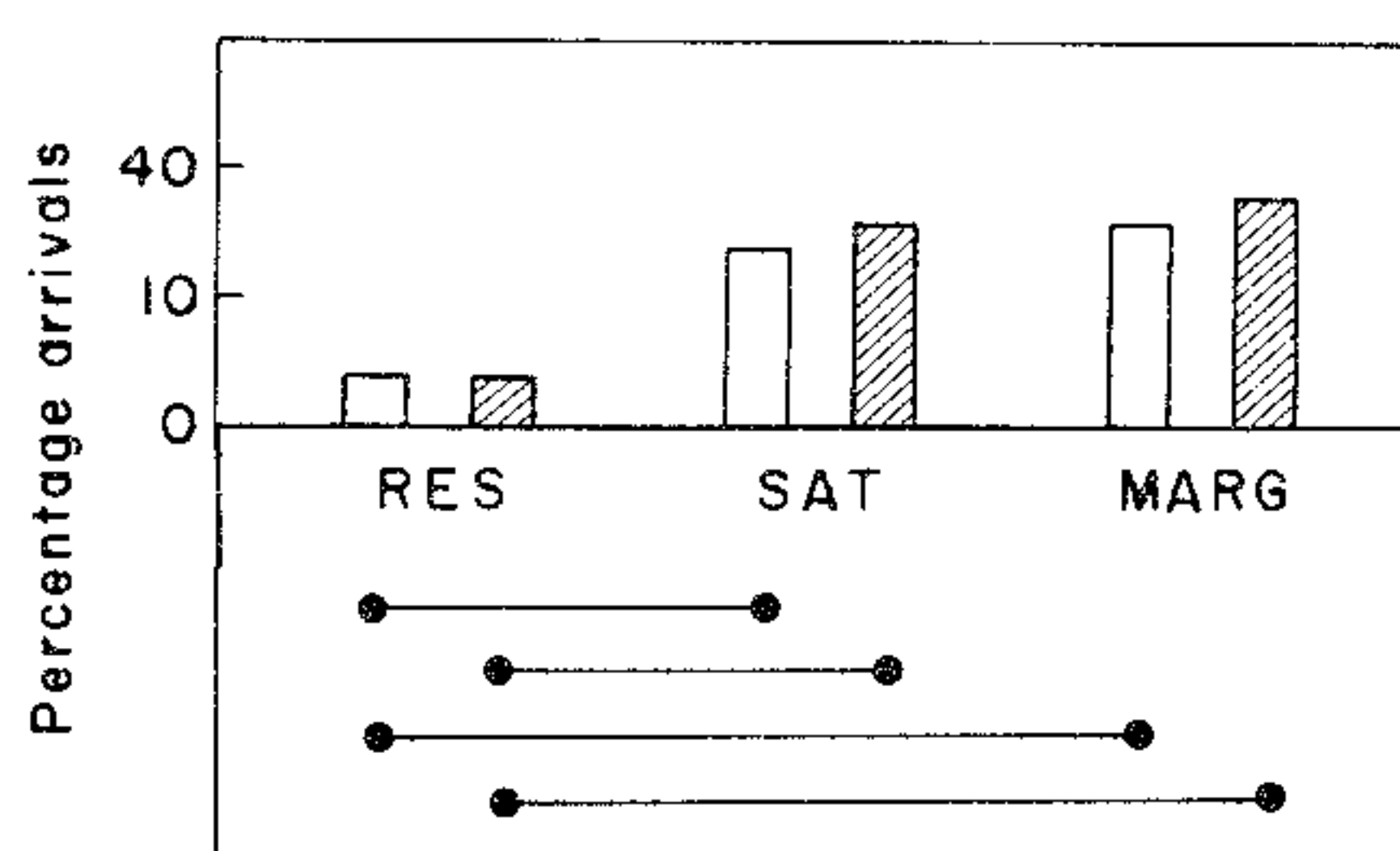


FIGURE 5. Percentage of arrivals (□) and departures (▨) by resident male Ruff, satellites, and marginal males, together with at least one Reeve. Horizontal lines indicate significant differences ($P < 0.05$).

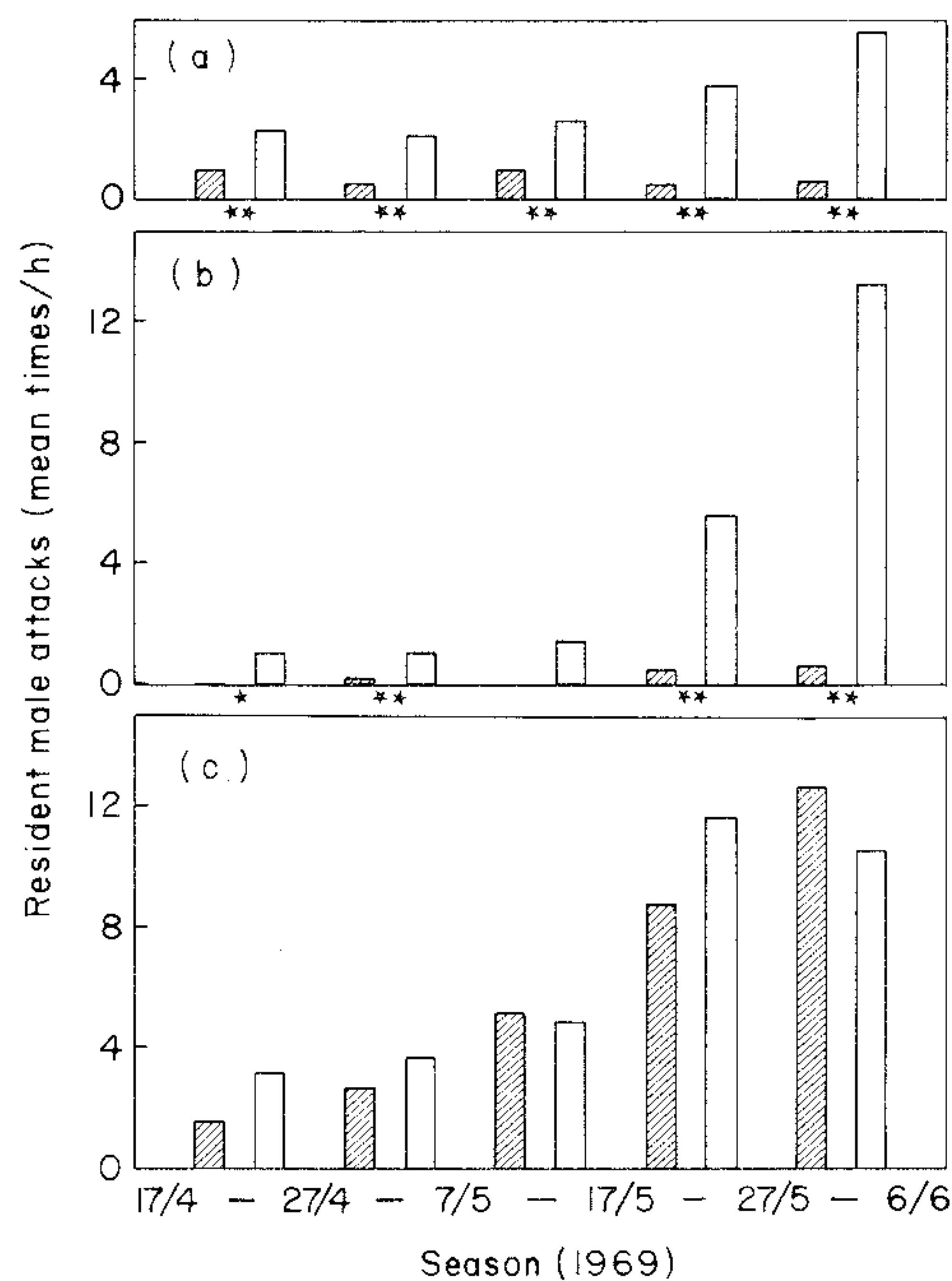


FIGURE 6. Mean number of times/h of being attacked by a resident male Ruff for resident males(a), satellites (b), and marginal males (c) during different parts of the season without Reeves on the lek (▨) and with Reeves present (□). * $P < 0.05$, ** $P < 0.01$.

indicates that at least some males do not spend all their time (apart from the necessary foraging trips) in visiting leks. Since these groups are not attached to certain areas, it is difficult to study their composition. It is clear, however, that both independent and satellite males occur in these groups. Since resident males spend almost all their time on their residences, it is unlikely that these males frequently visit such groups. Thus, by elimination, the great majority of independent males in temporarily displaying groups belong to the category of marginal males. Since marginal males seem to be more selective than satellites with respect to the conditions on the lek they visit, it seems plausible that on average a marginal male spends less time on leks (and more in temporary groups) than a satellite. The estimate of the proportion of satellites in a population on the basis of time spent on leks may therefore be affected in two ways: (1) by an under-representation of satellites and (2) by a probably stronger under-representation of marginal males. It is likely that both factors neutralize each other: that the time spent by independent males (resident + marginal males) is equally influenced by the time spent by satellites. It must be concluded, however, that the reliability of the estimate of the proportion of satellites in the population is still disputable.

COMPETITION BETWEEN MALES

In view of the concluding remarks in the previous section one might question again whether the concept of a mixed ESS leads to an understanding of the behaviour of Ruffs. To pose this problem more precisely, I want to consider the behaviour of males as a competition for a resource: insemination of females. Since the number of times females accept copulation is limiting, one might expect contests among males to divide this resource.

In the analysis of ESS's for conflicts between animals, a distinction was made between symmetric and asymmetric conflicts. In symmetric contests mixed strategies should be expected (Maynard Smith 1979). In asymmetric conflicts the asymmetry may be used as a cue to settle the contest (e.g., Davies 1978). Maynard Smith & Parker (1976) argued that in contests with perfect information about the asymmetry no mixed strategy can be an ESS.

In the Ruff confrontations between satellites and independent males are certainly asymmetric. Satellites do not possess a territory, they behave differently (Hogan-Warburg 1966, van Rhijn 1973), and in the majority of cases their status is exhibited by their plumage. Furthermore, other morphological features such as body weight (Dobrinskij 1969) may be different, independent males being heavier. In the Ruff collection of the British Museum (R. M. Gibson, pers. comm.), males with independent plumages had larger wings than males with satellite plumages. Table 2 shows that in the males I caught for ringing on Dutch leks (1968–71), wing length among resident males was significantly larger than among satellites ($P < 0.01$), but also larger than among marginal males ($P < 0.01$). Among independent males as a group, wing length was also larger than among satellites ($P < 0.05$). The differences between the plumage groups, however, were not significant. Within the group of independent plumages, wing length among resident males was larger than among marginal males ($P < 0.05$) and, within the group of atypical plumages, wing length among satellites was smaller than among resident males ($P < 0.01$) and than among independent males as a group ($P < 0.05$). These data suggest that, in the group of atypical plumages, body size (measured by wing length) is an additional factor determining male status (independent or satellite).

It is plausible that wing length is correlated with body size, and that body size is an important determinant for the probability of winning a conflict. Therefore it is likely that, on average, independent males have better fighting capacities than satellites. By using simple ESS models one should expect now that a conflict between a resident male and a satellite on the resident male's territory was settled on the basis of asymmetry cues in favour of the resident. Paradoxically most satellite copulations

TABLE 2

Frequencies of occurrence of different wing length (mm) among different categories of male Ruff trapped for ringing on leks

Plumage	Status	Wing length						Mean	n
		180	185	190	195	200	205		
Totals	Res	1	2	25	18	16	1	194	63
	Marg	2	3	13	6	2	0	191	26
	Ind	3	5	38	24	18	1	193	89
	Sat	2	2	2	2	1	0	189	9
Independent	Res	1	2	10	6	9	0	194	28
	Marg	1	2	7	2	0	0	189	12
	Total	2	4	17	8	9	0	192	40
Atypical	Res	0	0	15	12	7	1	194	35
	Marg	1	1	6	4	2	0	192	14
	Ind	1	1	21	16	9	1	193	49
	Sat	2	1	1	0	1	0	187	5
Satellite	Total	3	2	22	16	10	1	193	54
	Total	0	1	1	2	0	0	191	4

Note: Analysis of variance between categories: status (totals): Res > Marg**, Res > Sat**, Ind > Sat*; plumage (totals): no significant differences; males with independent plumages: Res > Marg*; males with atypical plumages: Res > Sat**, Ind > Sat*. * $P < 0.05$, ** $P < 0.01$.

occur on these small (mostly $< 1 \text{ m}^2$) territories in the close vicinity of the resident owner.

Van Rhijn (1973) and Shepard (1975) demonstrated that resident males may profit by the presence of (a) satellite(s) on their territories because females are more inclined to visit these residences. Thus, for a resident male, being tolerant with respect to satellites may enlarge his reproductive success. On the other hand, for a satellite, the property of investment of time in attending resident males would have never been developed if it were not associated with a positive influence on reproductive success. One may therefore consider the tendency of resident males and satellites to associate as influencing the resource, which is the number of females available for copulation. Hence, interactions between resident males and satellites cannot only be interpreted as a conflict for resources, they can also be conceived as a strategy that enlarges the accessibility of these resources. This could be an explanation for the maintenance of behavioural dimorphism in the Ruff.

ORIGIN OF THE SYSTEM

An explanation for the origin of this complicated system cannot be given on the basis of previous data. Mixed strategies should be expected in symmetric conflicts, and not in asymmetric ones. It may therefore be assumed that, in the evolution of the Ruff, differentiation in behaviour between independent males and satellites occurred before differentiation in morphological features, and/or satellites developed from males which were able to inseminate females without taking part in direct confrontations with other males. Gadgil (1972) demonstrated that 'sneaky' strategies may develop if the investment in devices of male competition becomes very high. The success per unit time of these sneaky strategies may be considerably lower than that of the competitive strategies, but the lifetime fitness may be similar because of a longer life expectancy (Selander 1965, Gadgil & Bossert 1970). Although at present the successes of independent males and satellites seem to be similar, it may be conceivable that the onset of the differentiation between both strategies occurred in the way suggested by Gadgil (1972). In order to come to a final conception of this differentiation process (in the last section of this paper), I first need to consider whether there are reasons for females to accept insemination by males whose qualities have not been tested in an inter-male competition.

DISTRIBUTION OF LEKS

It may be assumed that the behaviour and preferences of females strongly influence the spatial distribution of leks. It would be a maladaptive strategy for males to settle on leks which are visited rarely by receptive females. Males may be expected to behave in order to maximize their reproductive output, or to meet as many potential mates as possible.

In the Netherlands most leks can be found along the yearly migration route of Ruffs in areas which are suitable for breeding and foraging of Reeves (females). Nevertheless in these areas leks are far from regularly distributed. In my main study area in one season (1968) I found five leks, of which the most distant were only about 1 km apart. The shortest distance between leks was about 75 m. On the other hand, the nearest lek I knew outside this area was about 10 km away, although the area between seemed to be suitable for breeding and foraging. This picture of clusters of leks is fairly representative of the Dutch and Danish (Andersen 1948) situation.

The clustering of leks does not simply follow from the feeding and/or breeding habits of the females. During the pre-laying period, females sometimes forage in large groups. These groups seem to move considerable distances (probably dozens of km). They may include several males, which court now and then without being

attached to a particular place. Foraging groups may move in the close vicinity of a lek or a cluster of leks; however, they may also wander at great distances from leks. It may happen that some areas without leks are more often visited by foraging groups than some other areas around (clusters of) leks. During the laying and incubation period, females seem to forage alone in the vicinity of their nests, probably rarely farther away than 1 km. The nests can be found close to the leks (Andersen 1948) but, at least in the Netherlands, not in very large numbers. I also found nests and alarm-calling females at considerable distances from leks.

Bradbury (1979) obtained evidence by radio-tracking fruit-bats *Hypsignathus monstrosus* that leks were regularly distributed. Distances between leks approximated the diameters of female home-ranges. He therefore assumed that a female is not inclined to leave her feeding home-range for a short visit to a lek. He further assumed that she prefers males on large leks to males on smaller ones. Hence, the best strategy for males is to associate with as large a lek as possible, distributed over the whole foraging area of females of that species, but to maintain a maximum inter-lek distance of one female home-range diameter. I doubt whether this pattern occurs in the Ruff. The diameter of a Reeve's home-range during the phase of group foraging (in the pre-laying period) is larger than the distance between clusters of leks. The diameter of a Reeve's home-range during incubation is certainly larger than the smallest distance between leks. It is probably smaller, however, than the distance between clusters of leks. It seems unlikely that female home-ranges for foraging (as in the fruit-bat) determine the distance between leks. Besides, there is no evidence that Reeves prefer males on larger (clusters of) leks to males on smaller ones (Fig. 7). This graph, based on 29 early morning observations (0400–0700 h) on six leks in 1970 and 1971 (21 April–20 May), only suggests that female visiting rates are more variable on small leks than on larger ones.

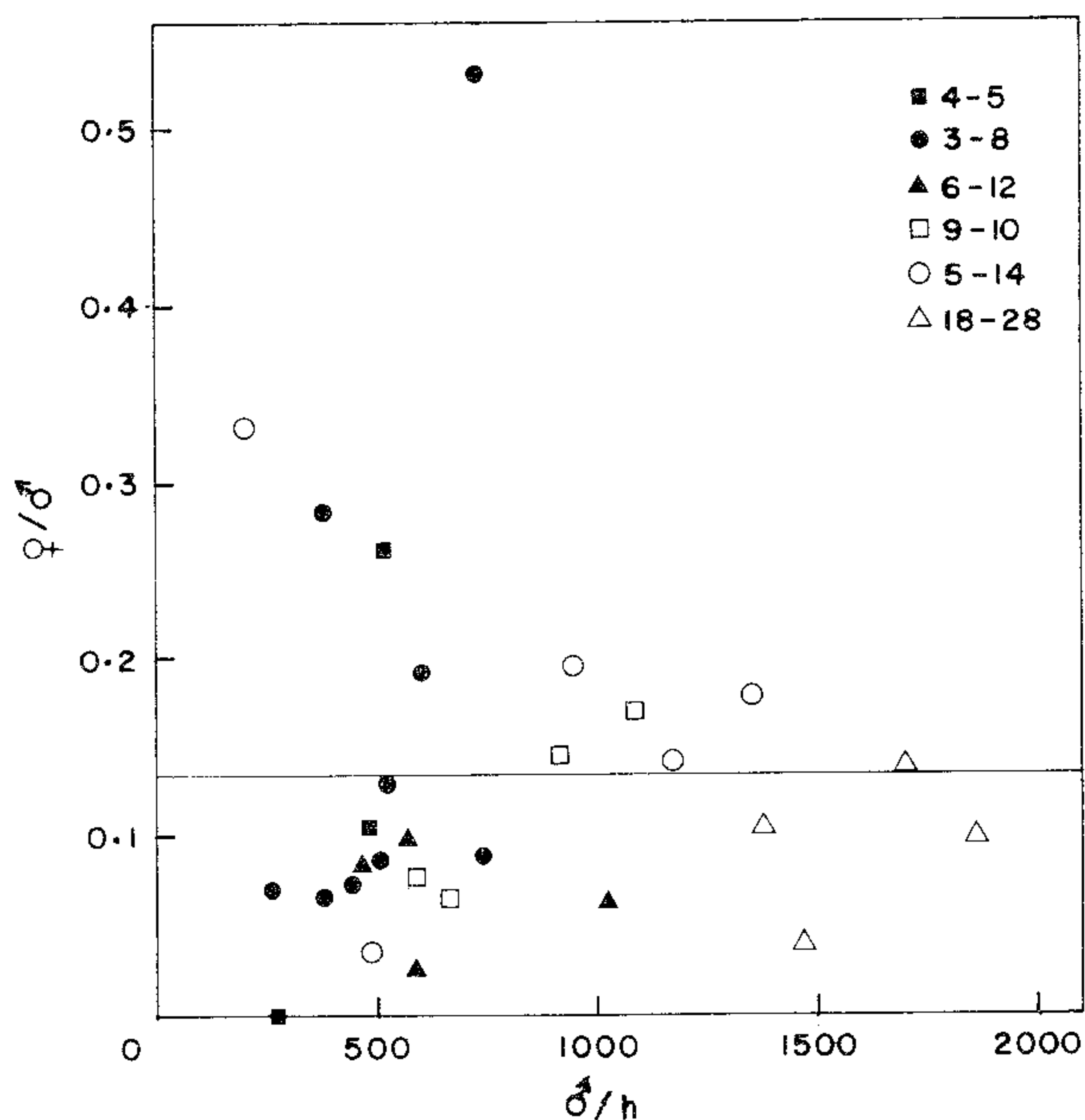


FIGURE 7. Total time spent by Reeves on the lek proportional to total time spent by all male Ruff (female/male) in relation to lek size expressed as total number of minutes/h spent by all males (male/h) on six leks. Number of resident male Ruff on the different leks is given in the upper right corner. The horizontal line represents the average proportion of Reeve's visiting time.

FEMALE COPULATION ACTIVITY

Every season during about two months (15 April–15 June) a large number of female visits to the Dutch leks can be recorded. Several females arrive alone, some females visit the lek in small groups, and females may also come to the lek in groups of over 20 individuals. Females mostly stay for a few minutes, but occasionally a visit may last longer than 1 h. In the majority of cases the females walk around the lek, stand for a moment near a particular male, preen their feathers, forage for a while, stand near another male, and leave the lek without copulating. In some cases the female may crouch and copulate.

On the most important lek I studied in 1969, I recorded 100 copulations; 45 of them were performed before 0900 h. In that season I observed about three early mornings per week (before 0900 h) on that lek, and about 14 h equally distributed over the rest of the day. I therefore estimated that about 380 copulations were performed on that lek in that season.

A score of 380 copulations is not equivalent to 380 fertilized females. Females may copulate several times during one visit. They may also pay several visits to the lek, during which they copulate. It is not difficult to give a rough estimate of the number of times a female copulates during one visit. On the basis of my own observations an average of two seems to be a reasonable approximation for visits with at least one copulation. It is much more difficult to estimate the number of times that a female visits a lek to copulate. For an observer it is almost impossible to recognize individual females during more than one visit. Fortunately I was able to record a number of visits of a few conspicuous females. From these observations I got the impression that individual females visit the same lek during a fairly short period (from a few days to a week). I suspect that three visits (during which on average two copulations occur) is a reasonable estimate. The score of 380 copulations would then be equivalent to 63 fertilized females during one season on one lek.

The lek which was responsible for the 63 fertilized females contained only about ten males (resident, satellite and marginal males) during female visits. On the other leks I studied I also got the impression that the number of females copulating on these leks was much higher than the number of displaying males. It would be possible for females to copulate on more leks. I have not been able to investigate this possibility, but I am sure that females may visit several leks. Nevertheless, I am rather convinced that the number of copulating females on Dutch leks is higher than the number of males on these leks.

FEMALE BREEDING DENSITY

It is very difficult to find a Reeve's nest but, from the number of alarm-calling females, it seems to be possible to obtain a reasonable idea of the breeding densities of Reeves. In the surroundings of the cluster of leks to which the lek with 380 copulations belonged, I found only five alarm-calling females by the end of the season. I scoured this area of about 4 km² carefully, so that I am almost certain that at least half the breeding females were counted. There were some other areas in the neighbourhood which seemed to be suitable for breeding, but which I did not explore. Taking their surface areas into account, I cannot imagine that more than 20 females were breeding in the domain of the investigated cluster of leks with at least 25 males. It is therefore likely that the number of breeding females in the Netherlands is lower than the number of males displaying on Dutch leks.

According to the above considerations, there seems to be a large discrepancy between the number of females copulating in the Netherlands and the number of breeding females. Two possible causes for this discrepancy can be given: first, a large

proportion of the fertilized females do not start breeding, and second, a large proportion of fertilized females do not stay in the domain of the (cluster of) lek(s) where these females copulated.

The first possibility does not seem to be biologically meaningful and therefore is unlikely. Why would females migrate to the north, copulate, and omit further breeding attempts? The only possible reason would be that breeding conditions are worse than expected, and that breeding attempts strongly decrease the chance of future reproduction. It is hard to believe that breeding is kept low by this factor year after year unless the recent breeding conditions have changed drastically. This last possibility cannot be rejected, since agriculture and animal husbandry have been modernized tremendously in the Netherlands over the last few decades. Nevertheless there are no indications that the ratio between males on leks and breeding females strongly changed during this time, although the absolute numbers declined. Thus, the hypothesis that a large proportion of fertilized females does not start breeding seems to be unlikely.

The second possibility, that a large proportion of the fertilized females do not stay in the domain of the lek, remains as the alternative hypothesis. This possibility could imply that females copulate on a large number of clusters of leks. It was impossible to test this. It could also imply that in the Netherlands many females breed far (several km) from the leks. In the Netherlands this only seems to occur exceptionally and the data for Denmark (Andersen 1948) and Germany (Mildenberger 1953) on nest distribution are incompatible with this idea. Finally, the hypothesis could imply that many females copulate during migration.

Reeves may breed far to the north: in Siberia up to 73°30'N. (Glutz von Blotzheim, Bauer & Bezzel 1975). It is possible that, in these northern breeding habitats, food conditions for the adults are suboptimal: males immediately return after the short courtship phase, and females return after failure of the brood. Consequently, for a Reeve it may be advantageous to start laying and incubation as soon as possible after arrival in the breeding area. In other words, she must try to find a father for her offspring while she is still able to find enough food for the formation of eggs and for the storage of reserves for the first difficult part of the incubation period.

GEOGRAPHICAL DISTRIBUTION

If some Reeves copulate during migration, differences can be expected in the geographical distributions of males and females. Males should prefer those places where females are inclined to copulate, instead of the areas where females are inclined to nest. It thus seems plausible that: first, males stay on average to the south of the nesting sites of the females, and/or second, the best males stay in the south of the breeding area and the other males move farther to the north to the less favourable copulation places. The first possibility implies that the sex ratio changes with geographical latitude, and the second that the copulation frequency per male changes.

The hypothesis concerning the geographical distribution of the sexes can be related to the behavioural dimorphism of the males. It is likely that reproductive success is not dependent on the same factors for northern and southern males. Northern males should be specialized in the tracing of unfertilized females breeding locally, southern males should be specialized in the luring of receptive females on migration. I am inclined to believe that the satellite strategy (with a good deal of wandering around) is adapted for the tracing of females in an area with a low breeding density. The resident strategy seems to be adaptive for the luring of migrating females. Leks with many resident males are very conspicuous and perfectly visible from the air. They are settled in open areas near water (Siedel 1960)

on slight elevations in a smooth landscape (Bancke & Meeseburg 1952, Mildemberger 1953) in the close vicinity of suitable foraging grounds for the females. Leks seem to occur particularly along the migration routes of birds going north. Thus, a male in the southern part of the breeding area seems to behave optimally if he joins other males on a lek or, if he is unable to settle on an existing lek, to stay in the neighbourhood of a lek together with other males to benefit from the luring effect of the old lek.

This theory predicts that the proportion of satellites (white or light coloured males) should increase with geographical latitude. A few data in the literature support this prediction. Lindemann (1951) suggested that the proportion of white males increased from south to north and from west to east in the Baltic region. He associated this change in the proportion of white males with differing durations of snow cover in these areas. Drenckhahn (1975), however, argued that the proportion of white males does not change in a systematic way with geographical latitude, although considerable differences seem to exist between various regions. In my opinion there are a few weaknesses in his analysis. First, part of his data was based on skins (e.g., from Siberia) collected by hunting and part of it was based on field observations (e.g., from the Netherlands and Sweden) on leks. It is likely that different selections were made by these differing techniques (cf. Table 2). Secondly, different observers may use different criteria for classifying plumages and, thirdly, it is possible that the attachment of satellites to leks also changes with geographical latitude. In any case, the proportion of white males on Dutch leks indicated by Drenckhahn (30–44%; derived from Hogan-Warburg's descriptions), seems to be much higher than the real proportion of satellite males in this population (about 13%). Thus, the basis of Drenckhahn's conclusions seems to be rather weak and provides no evidence leading me to reject my hypothesis on satellite distribution.

EVOLUTIONARY SPECULATIONS

In a preceding section it has been argued that the differentiation in behaviour between independent males and satellites occurred before differentiation in morphological features, and/or that satellites developed from males which were able to inseminate females without taking part in direct confrontations with other males. In this last section some speculations will be made about differentiation processes on the basis of known facts on social systems in related species (family Scolopacidae, in particular the sub-family Calidrinae), and the ideas formulated above on mating and migration in the Ruff.

In most species of the family Scolopacidae males defend territories during the reproductive period. In a few polyandrous species (e.g., the Spotted Sandpiper *Actitis macularia*: Hays 1972, Oring & Knudson 1972, Oring & Maxson 1978) territorial behaviour is performed mainly by the female. Lek behaviour is rather common in this family: in the Calidrinae it also occurs in the Buff-breasted Sandpiper *Tryngites subruficollis* (Oring 1964) and elements of it can be found in the Pectoral Sandpiper *Calidris melanotos* (Pitelka 1959) and White-rumped Sandpiper *Calidris fuscicollis* (Parmelee, Greiner & Graul 1968); in the Gallinaginae it occurs in the Great Snipe *Gallinago media* (Ferdinand 1966, Ferdinand & Gensbøl 1966). Sexual dimorphism is very common within this group, but not so extreme as in the Ruff. In many species, however, the female is larger than the male (Pitelka, Holmes & Maclean 1974), particularly in the polyandrous species.

It is likely that the Ruff evolved from a species with a simple lek system, like its close relative the Buff-breasted Sandpiper (Oring 1964) in which all males behave similarly and have similar morphological features. In species with lek systems, characters related to inter-male competition are supposed to be strongly affected by

selection (Trivers 1972, Emlen & Oring 1977). Body size is such a character: both the extreme sexual dimorphism and the large size in relation to other Calidrinae may be associated with these selection pressures. Besides, time spent on a lek may be another important factor in inter-male competition.

It is also likely that the Ruff's ancestors, like its relatives, courted and copulated in the same areas where they nested, and that these breeding areas were located in the boreal, sub-arctic and arctic regions, as in the other members of the Calidrinae (Pitelka *et al.*, 1974). In these areas food mainly consists of small items, like larval and adult Diptera, which may be very abundant during summer (Holmes 1970, MacLean & Pitelka 1971). For chicks this food situation seems to be perfect. An adult Ruff, however, one of the largest species of the Calidrinae, has to spend much time collecting food. In these areas it seems to be impossible for a large male to spend much time on a mating territory without food. Consequently, during the process of evolution inter-male competition in the northern part of the breeding area would be limited by the food conditions for the adults. On the other hand, in the southern part of the breeding area where there are larger food items inter-male competition could be more extreme.

If the hypothesis of strongly competing males in the south and moderately or non-competing males in the north is correct, then females have several options for their reproductive behaviour. In the south they could easily select a good quality male, but would have to be content with sub-optimal conditions for chicks; in the north it would be very difficult for them to select a good quality male, but the conditions for chicks are better. So today, in the south of the breeding area, one may expect that a few good quality males perform almost all copulations. On the Dutch leks one male often performs more than 50% of the copulations. In the extreme north copulations may be expected to be distributed more evenly among males. Thus for a strong male it must be advantageous to stay in the south and to compete with other males. This could even result in a better average quality of males in the south than in the extreme north. Under these conditions it would pay for females to develop the habit of mate selection in the south and nesting in the north.

If, during the same evolutionary process, competition among males influenced reproductive success only poorly, one might expect that non-competitive morphs accompanying females in foraging flocks were, during their whole life-time (Gadgil 1972), at least as successful as competitive morphs. This could be the origin of the satellite strategy in the Ruff. When the good quality competitive morphs stayed in the south of the breeding area and the average quality of the competitive morphs in the north went down, it would become advantageous for the non-competitive morphs in the north to distinguish themselves from the competitive morphs in order to signal that their average quality was better. This could be the origin of the morphological differentiation between satellites and independent males. It is here recalled that normally adult satellites have white heads during the whole year, while the winter plumages of independent males resemble female plumages.

As, by an increase of male quality and by the development of the female's capacity to copulate on migration, southern leks became more attractive for females, the non-competitive males would have had to improve their reproductive strategy. Perhaps by accompanying females visiting the leks and by adopting submissive postures, they were able to avoid direct attacks by resident males. Besides, satellites could be exploited by resident males for the attraction of females to the lek and to the residences. However, such an exploitation would never have evolved if it were not associated with reproductive advantages for satellites: a share in the insemination of females. In fact, the relation between both categories of males can be considered as reciprocal altruism (Trivers 1971). Since the satellite always performs its altruistic act

TABLE 3

Diversity in basic colours of ruff (neck plumage) and head-tufts of 214 male Ruff described by Hogan-Warburg (1966: table 13)

Ruff	Head-tufts											
	All males				Independent males				Satellite males			
	B	H	W	Tot	B	H	W	Tot	B	H	W	Tot
Black	41	14	5	60	41	11	5	57	0	3	0	3
Hue	14	31	1	46	14	25	0	39	0	6	1	7
White	21	31	56	108	21	4	11	36	0	27	45	72
Totals	76	76	62	214	76	40	16	132	0	36	46	82
Information estimates as measures of diversity												
	All				Independent				Satellite			
H' (ruff)	1.50				1.56				0.66			
H' (head-tufts)	1.59				1.35				1.01			
H' (ruff, head-tufts)	2.81				2.71				1.60			

(providing females) before the resident male is able to reciprocate (tolerating the satellite to copulate), satellite males had to evolve a mechanism against cheating by resident males. This could be done by selecting only readily identifiable resident males (Trivers 1971, van Rhijn & Vodegel 1980, van Rhijn 1980, Axelrod & Hamilton 1981). This could be an explanation for the extreme polymorphism in plumages of independent males. Measures of diversity (information estimates: e.g., Pielou 1977) are higher for independent males than for satellites (Table 3). These measures were based on only three groups of primary colours of ruff and head-tufts. If these colours were further specified and patterns with secondary colours were incorporated, the difference would certainly be much more pronounced.

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