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SOCIAL BEHAVIOR OF THE RUFF, PHILOMACHUS PUGNAX (L.)

by

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I. Introduction

A. Scope of the Study

The Ruff, *Philomachus pugnax* (L.), differs from other waders in its breeding behavior: courtship and mating take place on a communal display ground or lek; no sounds are uttered during these activities; nesting behavior, incubation, and parental care are the exclusive task of the female. The Ruff is also distinguished by its sexual dimorphism in both size and plumage, and by the extreme individual diversity in the male nuptial plumage.

The earliest published accounts of behavior on the lek are those of Selous (1906, 1907), a pioneer in the field study of bird behavior. Interested in the Darwinian concept of sexual selection, Selous objectively described the interactions among the individual males and females on the lek in an attempt to gather information on partner choice on the lek and, specifically, on the function of fighting among the males. His descriptions and interpretations of this behavior are remarkably good,

considering the date at which they were made. Other accounts of field studies on the breeding behavior of the Ruff have since been published (PORTIELJE 1931; ANDERSEN 1944, 1948, 1951; LINDEMANN 1951; BANCKE & MEESENBURG 1952, 1958; MILDENBERGER 1953), and a number of authors have made comments on different aspects of the Ruff's breeding behavior (e.g., CHRISTOLEIT 1924; ARMSTRONG 1947; TINBERGEN 1959; WYNNE-EDWARDS 1962). VAN OORDT and JUNGE (1934, 1936) have investigated the endocrinological aspects of the development of the male nuptial plumage. LINDEMANN (1951) and GOETHE (1953) describe and comment on the extent of the plumage diversity among the males.

The present study extends the observations on the lek behavior and morphological features in the external appearance of the Ruff. Specifically, this is an ethological study of the lek behavior of the Ruff which investigates the social organization of the lek community and the behavior patterns that serve mutual communication among the birds. It is assumed that the behavior patterns provide many clues for the understanding of the social organization. Further, particular attention is paid to the biological significance of the plumage diversity within the lek community. Accidentally, this study revealed that the Ruff presents an extreme example of behavioral polymorphism: it appears that within the male community two groups of males coexist which show distinct differences in behavior. In a complicated way these behavioral differences are associated with differences in the external appearance of the individual males.

This paper is organized in the following manner. Descriptive data on morphological features in the external appearance of the Ruff are presented in Chapter II. Mutual relations within the male community, correlations of behavioral differences with external appearance, and the intersexual relations during courtship are dealt with in Chapter III; the typical situations on the lek in which the behavior patterns occur are also described in this chapter. Detailed descriptions of the form of these behavior patterns are presented in Chapter IV. Chapter V is concerned with a discussion of different aspects of the behavioral polymorphism and the plumage diversity in the male Ruff.

B. TAXONOMY AND BIONOMY

The Ruff is the only representative of the genus *Philomachus*. This genus belongs to the *Charadrii* which, according to WITHERBY *et al.* (1952), with the *Lari* and some other groups constitute the order of the

Charadriiformes. These authors also state that the relationship of *Philomachus* to the genus *Calidris* is fully established by LOWE (1915a and b) on the basis of characters of plumage pattern in nestlings and skull morphology. PITELKA (1959) has discovered that among the *Erolia* species—WITHERBY *et al.* include the genus *Erolia* in the genus *Calidris*—especially *E. melanotos* and to a less degree also *E. fuscicollis* show many similarities with *Philomachus* with respect to their breeding organization and sexual dimorphism. According to PITELKA these similarities provide strong arguments for a relatively close relationship and common origin of these *Erolia* species and *Philomachus*. More recently, PITELKA (personal communication) has studied the behavior of *Tryngites subruficollis* and found that it is even more similar to *Philomachus*. He suggests that the three species, *melanotos*, *subruficollis*, and *pugnax* form a step-wise sequence of evolution of a social system.

The Great Snipe, *Capella media*, is the only other species among the waders in which courtship takes place on a communal display ground. In contrast to the Ruff this species is very noisy on the lek. Apparently the lek system in both species is due to a convergent development.

The Ruff is a migratory bird: its breeding areas are in northern Europe and Asia and the species winters in Africa and south Asia (WITHERBY *et al.*) The habitat during the breeding season consists of grassy marshes and moist meadows. Outside the breeding season the species lives either in a rather similar habitat or frequently on the muddy borders of lakes and rivers; it is also seen frequently, but less regularly, on muddy sea shores. During the breeding season the food consists mainly of insects of different kinds, worms, fresh water molluscs, and seeds (WITHERBY *et al.*). In the breeding areas I observed different ways of feeding. While walking through the meadows they feed by boring the bill into the wet ground (worms); pecking on the ground (walking insects and seeds); predating on flying insects which visit the flowers between the grasses. While standing in shallow water they feed by probing the mud of the bottom (molluscs, worms).

C. MATERIAL

This study has been carried out in the field. Leks in 4 different areas of the Netherlands have been examined; the approximate location of these areas is shown on the map in Figure 1. The number of days spent in observation in each area during each season is given in Table 1.

There was more than one lek in each of the four areas observed. The distance between leks ranged from about 50 meters to a few hundred

meters; this means a flying time of at most a few minutes for the birds. Eight leks have been studied in total, some of them in successive years. During the course of these observations, the leks were always situated in practically the same location in the meadows from year to year. The

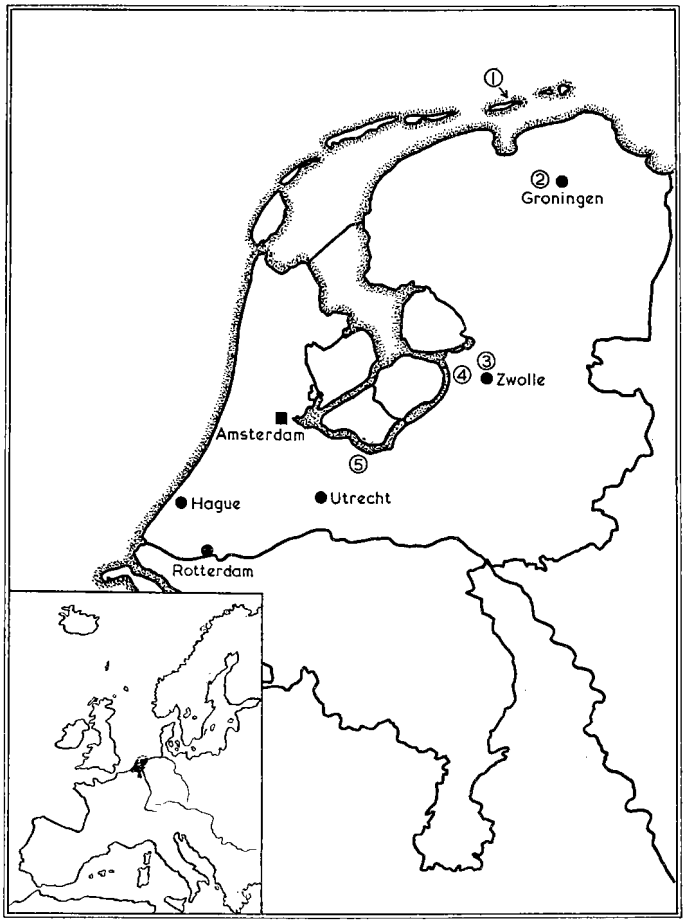

FIGURE 1. Map of the Netherlands showing the locations of the leks observed.
1: Schiermonnikoog
2: Roderwolde
3: Hasselt
4: Oosterwolde Polder
5: Eem Polder

number of leks located in each area during each season is given in Table 2. In 1960 there were two leks on Schiermonnikoog, and a few birds were

TABLE 1

NUMBERS OF DAYS SPENT IN OBSERVATION

		Schier.	Roderwolde	Hasselt	O.P.
1960	March	4			
	April	23			
	May	27			
	June	22			
	July	2			
1961	March	4		0	
	April	22		0	
	May	22		6	
	June	13		2	
1962	April	19	3	0	0
	May	0	5	9	15
	June	6	6	0	0
1963	April	4			

TABLE 2

NUMBER OF LEKS IN EACH AREA

	Schier.	Roderwolde	Hasselt	O.P.
1960	2	—	—	—
1961	1	2	2	2
1962	1	2	3	2
1963	1	—	—	2

regularly found on a third site. According to residents of the island, a lek had been located on this site in former years. From 1961 on, only one of the leks was populated, although some of the birds still showed an attachment to the other two sites.

All the leks studied were situated in moist meadows which were criss-crossed by ditches. All were located at the border of a ditch or of a wider water surface. A few of the leks were situated on a slightly higher level than the surrounding land.

On Schiermonnikoog, field observations were started early in the season: in 1960 on March 27 and in 1961 on March 21. These early observations revealed that many of the males had already arrived in March and that more arrived in the first few days of April, whereas the first records of females in 1960 and 1961 were April 6 and April 7, respectively. These observations confirm the statement by WITHERBY *et al.* that males arrive before the females in the breeding grounds. Four individually recognizable males on Schiermonnikoog in 1960 could be

distinguished as younger males by features in their external appearance (cf. Section II.B.). The first records of these 4 males were made between April 14-18. This confirms the statement by WITHERBY *et al.* that older males arrive before the younger ones on the breeding grounds.

After their arrival in the breeding area, males are seen in small groups moving through the meadows foraging. Later, females may be seen in such foraging groups. The first observations of birds visiting the lek were made on April 7 in both 1960 and 1961: in both years the first visits to the lek were closely synchronized with the arrival of females.

At the beginning of the season groups of males or mixed groups land on the lek only irregularly. They stay there only for short periods during which some interactions may be shown, but suddenly they fly up again as a flock and resume their foraging in the field. As the season progresses, flocking gradually diminishes in frequency and the males occupy the lek more continuously. Flocking behavior in alternation with visits to the lek has also been noted by SELOUS (1906, 1907) and BANCKE and MEESENBURG (1958). On Schiermonnikoog, the leks were regularly populated in April, May, and the first part of June. In the Netherlands, the greatest amount of activity on the lek is shown from about the middle of April until the end of May, with some variation from season to season.

After their nocturnal absence, males start to arrive on the lek shortly before dawn when it is still completely dark. The diurnal activity reaches its highest level in the early morning hours with a peak shortly after sunrise. In the late morning there is a lull during which the birds go foraging. From the middle of the day until early evening the lek is populated again. BANCKE and MEESENBURG (1952) have examined the daily fluctuation in activity on the lek in some detail.

Leks show considerable variation in size. The size is dependent on the number of resident males, the category of males which forms the stable population of a lek (cf. Chapter III). On most of the leks studied, the number of resident males present at the same time varied between 3 and 8. In Hasselt in 1961, however, one lek was occupied by 15 resident males, and in the Oosterwolde Polder in 1962 one lek had 19 resident males. The first category of leks will be referred to in the text as the small leks, the second category as the large leks. Leks of even larger size do exist. FEEKES (personal comm.) observed a lek in the Eempolder (see the map in Fig. 1) in 1961 on May 29 and 31 on which 24 resident males appeared to be present. MILDENBERGER (1953) who reports about a new settlement of Ruffs in an area near Wilhemshaven (NW Germany)

distinguished 4 separate display sites, three of which were regularly occupied by only one male each, and the fourth by only two males. In the later observational years on Schiermonnikoog the number of males present had diminished greatly and at that time also on Schiermonnikoog display sites occupied by only one or two males were established (cf. Section III.B.4).

At the time that the males started to populate the leks regularly, females began their solitary life in the fields. The nests which were found on Schiermonnikoog were lying in the meadows surrounding the leks. Important information about the choice of nest site, nest building and incubation by the females and about eggs and young in the nests is presented by ANDERSEN (1944, 1948, 1951) and by MILDENBERGER (1953)

Several male Ruffs, collected as adults from different sources, and 3 young females, raised from eggs hatched in an incubator, were kept in confinement at the Zoology Laboratory of the University of Groningen.

D. OBSERVATION TECHNIQUE

Observations were carried out from a hide of one cubic meter placed at a distance of at least 10 meters from the lek. A hide set up at closer distances usually interferes with the normal behavior of the birds on the lek.

Field glasses (8 × 40), a notebook, and a tape recorder were used for making and recording the observations. Photography was used to allow a more detailed study of the behavior patterns of the birds. Pictures in the text are drawn after 35-mm slides made with the use of a 40-cm telephoto lens, and after frames of a 16-mm movie film.

I was normally in the hide before dawn and continued observations until activity on the lek reached a low level—this frequently did not occur until 9 or 10 during the middle of the season. On many occasions I also made observations for a few hours during the afternoon.

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II. MORPHOLOGICAL FEATURES IN THE EXTERNAL APPEARANCE

A. SEXUAL DIMORPHISM

Very marked sexual dimorphism exists in both size and plumage. Males are larger than females and develop a distinctive nuptial plumage. This is characterized by a large pectoral ruff, two tufts on top of the head, long ornamental feathers in the upper parts and small wattles on the forepart of the head between bill and eyes. The pectoral ruff and head tufts are formed by long feathers; those of the ruff emerge from a continuous area including chin, throat, cheeks, and two parallel longitudinal strips in the neck; those of the headtufts emerge from the crown. The nuptial plumage shows great individual diversity with respect to color and pattern of the nuptial feathers and color of the wattles. The plumage diversity of the males makes it easily possible for a human observer to recognize males individually.

Females also develop a nuptial plumage. This plumage is only slightly different from the winter plumage: it is distinguished by the feathers of the head and front part of the body and by the feathers of the upper parts which have a brighter and more conspicuous pattern. Also, the nuptial plumage of the females shows individual diversity, though to a much smaller extent than that of the males. It is shown in the spot pattern of the feathers of the head and throat, and in some individual females the

feathers of the upper parts have colored rims instead of gray. The difference between the winter plumage and the female nuptial plumage can be easily seen in comparing Plate 49 with Plate 56 in TINBERGEN (1959). I found the slight diversity of plumage among females insufficient to recognize individual females that visit the lek. In the three years of observation I have noticed two individual females which had developed a few long feathers emerging from the throat in a way similar to male nuptial feathers.

MAUERSBERGER (1957) states that the nuptial plumage of the females corresponds completely with the prenuptial plumage of the males which is a shortlasting plumage into which they moult in February and March and which is replaced by the nuptial plumage shortly before the onset of breeding. He found that the prenuptial plumage is just as variable as the female nuptial plumage. His work is based on a study of museum specimens. The early observations in 1960 showed that males may arrive in their breeding area before the nuptial plumage has started to develop, whereas the early observations in 1961 suggested that the nuptial plumage had started to develop before their arrival.

Almost all of the males on Schiermonnikoog in 1960 reached their optimal plumage development by April 25; this was judged by the length and brilliance of the nuptial feathers and wattles. Four of the total 24 males, however, were considerably later in reaching their optimal development; these four males did not reach optimal development until between May 8 and 27. After reaching their optimal development, no obvious change in the nuptial plumage was noticeable until the end of the season when the males started to shed their nuptial feathers. The exact time of shedding varied among the individual males. The earliest notation was a male that had shed most of his ruff feathers on June 4 in 1960; in 1961, this particular male developed wattles before all other males. Shortly before shedding starts, the ruff feathers develop a frayed appearance. The four males which reached their optimal development later in the season than the others were among the ones that still had an intact plumage on June 24, the last day of observation on the lek. Thus, individual males vary slightly in the timing of the seasonal development of their nuptial plumage.

B. Effect of Age on the External Appearance

From Ruffs kept in confinement it is a well-known fact that in the course of seasons the size of ruff and head tufts increases. This indicates that males with a small size plumage are younger than the ones with a

larger size plumage. The increase in size of plumage over the course of seasons has been confirmed by the field observations on Schiermonnikoog: five of the 24 males in 1960 had a nuptial plumage of a distinctively smaller size. These five males were also present in both 1961 and 1962; all five increased the length of the nuptial feathers noticeably, one having a fully developed plumage in 1963. The four males on Schiermonnikoog in 1960 mentioned above that developed their nuptial plumage relatively late in the season all belonged to the group of five males with underdeveloped nuptial plumage (no accurate record of the seasonal development of the fifth male was made). Thus, young males are characterized by an underdeveloped nuptial plumage and by a relatively late seasonal development. This suggests that the male on Schiermonnikoog with a fully developed plumage and a distinctively earlier seasonal development and moult might have been an older male; and that, in general, early seasonal development and moult are characteristic of older males.

Six of the 15 satellite males (see Chapter III for the term satellite) distinguished on the two leks in Roderwolde differed in the area covered with wattles. The area was extended to far behind and above the eyes and also the triangular area between the eyes was covered with wattles instead of the usual short feathers. Such satellite males were also seen on the large and small lek in the Oosterwolde Polder, but not on Schiermonnikoog. This feature was only seen in satellite males with very long nuptial feathers and not in satellite males with underdeveloped nuptial feathers; it was never seen in independent males (see Chapter III). Thus, such an enlarged area with wattles is apparently characteristic for relatively old satellite males.

ANDERSEN (1951) has pointed at another characteristic dependent on age, namely the color of the legs. Nestlings have lead-gray legs and in the course of seasons a gradual color change takes place in most individuals going through greenish-gray and reddish-green and ending in a reddish or orange color. The color change has been determined by ANDERSEN by recaptures of both males and females in successive seasons. This color change has been confirmed by my observations on three females which hatched in the incubator and were kept in confinement for more than three years. Further, a similar change in the color of the bill may take place. In two of the three females the color of the legs changed gradually to a reddish color by the third year after hatching; in these two females, the color of the bill did not change. In the third female both the legs and the base of the bill changed to a reddish color the first year after hatching, whereas the very tip of the bill remained

lead-gray. Thus, it is likely that there is considerable individual variation in the speed of color change through life. These data further suggest that other factors in addition to age influence color changes in the legs and bill. Observations on males in the field also confirm this idea. Of 68 males for which complete descriptions are available, 45 had both reddish legs and bill, 22 had reddish legs, but a lead-gray bill, and 1 had both lead-gray legs and bill. No bird was ever seen with a red bill and gray legs, which suggests that the bill never changes color before the legs. Further, of the 45 males with both red legs and bill, 8 were definitely young males as judged by the size of their nuptial feathers; of the 22 males with red legs and gray bill, 15 were definitely older males by the same criterion. Thus, these field records show the individual variation in the speed of color change through life.

An additional factor that affects change of color in the legs and bill appears to be associated with plumage color: all older males with black feathers in their plumage had a gray bill, while the young males without black nuptial feathers may already have red legs and a red bill.

C. Diversity in the Male Nuptial Plumage

Plumage diversity among males exists in the color and pattern of the nuptial feathers of ruff, head tufts and to a less extent in the wing coverts and in the color of the wattles. The plumage has been described, except for the wing coverts for about 200 males on the leks in the four observation areas. In the following analysis of the plumage diversity, numerical data will be presented only for the plumages of the 29 males on Schiermonnikoog in 1960 and 1961.

The plumages of the individual males vary in a number of dimensions: (1) the basic and secondary color(s) in ruff and head tufts, (2) the pattern in ruff and head tufts, (3) the contrast between ruff and head tufts and (4) the color of the wattles. In order to give some idea about the extent of the plumage diversity, I will describe the values each dimension can assume, and the combinations of values of the three dimensions that occur in the ruff and head tufts. In addition, I will describe, under the heading "contrast of ruff and head tufts", to what extent variations in the ruff and head tufts are independent. Finally, the extent to which the color of the nuptial feathers and wattles vary independently will be described.

(1) *Basic and secondary color(s) in ruff and head tufts*

The basic and secondary colors of the ruff and head tufts vary from

TABLE 3

OCCURRENCE OF DIFFERENT VALUES DISTINGUISHED AS BASIC AND SECONDARY COLORS OF RUFF AND HEAD TUFTS, ARRANGED ACCORDING TO INCREASING BRIGHTNESS (+ = observed; — = not observed)

	Basic color		Secondary colors	
Value	Ruff	Head tufts	Ruff	Head tufts
Black	+	+	+	+
Dark gray	—	+	+	+
Dark brown	+	+	+	—
Dark brownish red	+	+	+	—
Light brown	+	+	+	+
Orange	+	+	+	+
Light red	—	—	+	—
Yellowish brown	+	+	+	—
Reddish beige	+	—	+	+
Beige	+	+	+	+
White	+	+	+	+

black through brown, red, and yellow, to white. Specific values of these colors are listed in Table 3.

Among the 29 males on Schiermonnikoog in 1960 and 1961, black, various hues, and white were the basic color of the ruff and head tufts in the proportions 10:7:12 and 10:11:8, respectively (black included dark gray in the case of the head tufts). These data show that in both ruff and head tufts, black and white are the most common color, while the other colors are relatively less frequent. This also appears to be true for the other observation areas.

Ruff and head tufts may be plain or may contain one or two secondary colors; in the 200 plumages described, I never saw more than two secondary colors. The frequency of occurrence of secondary colors in the ruff and head tufts of the 29 males on Schiermonnikoog in 1960 and 1961 are given in Table 4. These data show that males with plain tufts

TABLE 4

FREQUENCY OF OCCURRENCE OF SECONDARY COLORS AMONG MALES ON SCHIERMONNIKOOG IN 1960 AND 1961

	Number of males	
	Ruff	Head tufts
Plain	9	14
One secondary color	14	14
Two secondary colors	6	1
Total	29	29

TABLE 5

FREQUENCY OF OCCURRENCE OF COMBINATIONS OF BASIC AND SECONDARY COLOR(S) IN RUFF AND HEAD TUFTS AMONG MALES ON SCHIERMONNIKOOG IN 1960 AND 1961

Combination of basic and secondary color(s)	Number of males	
	Ruff	Head tufts
Black plain	3	5
+ hue	2	2
+ white	2	2
+ hue and white	3	1
	10	10
Hue plain	1	5
+ black	0	2
+ hue	5	4
+ white	0	0
+ two secondary colors	1	0
	7	11
White plain	5	4
+ black	3	3
+ hue	2	1
+ black and hue	2	0
	12	8

are more frequent than males with plain ruffs. This is also true among males in the other observation areas. Two secondary colors are relatively infrequent. In all cases of two secondary colors, one is either black or white, while the other may be black, white or any of the hues. The combinations of the various values of basic color and secondary colors and their frequencies in the ruff and head tufts among the 29 males are presented in Table 5. The combination of a colored ruff with black markings, absent on Schiermonnikoog, did occur in other areas. The other combinations not represented on Schiermonnikoog were also not seen in other areas.

(2) *Pattern in ruff and head tuft*

Patterns in ruff and head tufts occur due to the presence of secondary colors. Three different patterns have been distinguished.

(1) Transverse striping, in which the feathers show transverse stripes or bars; this pattern occurs in both ruff and head tufts.

(2) Spots, irregularly shaped blotches caused by one or a group of

differently colored feathers or by multi-colored feathers; this pattern occurs in both ruff and head tufts.

(3) The bib: zones of different color, in which the top feathers of the front part of the ruff just below the chin form an area of differently colored feathers. In some cases the bottom feathers of the ruff form a third zone of differently colored feathers. This pattern can easily be overlooked, however, since the bottom feathers are normally covered by other ruff feathers. This pattern will therefore not be included in the description of plumage diversity.

Further, combinations of transverse striping and spots, and of transverse striping with a bib occur.

The frequencies of the different patterns and combinations of patterns in ruff and head tufts among the 29 males on Schiermonnikoog are presented in Table 6. It can be seen in the table that patterns are more

TABLE 6

FREQUENCY OF OCCURRENCE OF PATTERNS AND COMBINATIONS OF PATTERNS IN RUFF AND HEAD TUFTS AMONG MALES ON SCHIERMONNIKOOG IN 1960 AND 1961

Pattern	Number of males	
	Ruff	Head tufts
Plain	9	14
Transverse striping	8	7
Spots	9	8
Striping and spots	0	0
Bib	2	—
Striping with bib	1	—
Total	29	29

frequent in ruffs than in tufts, and that transverse striping and spots are the most common patterns in both the ruff and head tufts, while the bib and combinations of patterns occur very infrequently.

Transverse stripes are evenly distributed over the whole surface of ruff or head tufts. In general, the striped pattern consists of only one secondary color on the basic color. In only one case out of about 200 were there two secondary colors involved: black and white. There are two variables involved in transverse striping: the density of the stripes or bars, and the width of the bars. These variables do not vary independently of each other: dense striping usually consists of narrow bars, the extreme case of which has the bars of the basic color and the secondary

color the same width. In this case it is arbitrary which of the two colors is called the basic color, but I have consistently called the darker color the basic color, since this one is visually the most impressive.

The male mentioned above with two secondary colors in his ruff also differed from normal transverse striped males in that only the median part of his ruff feathers had transverse stripes and not the edges. The effect of this was that the ruff had both a transverse and a longitudinal pattern. This was the only such case noted.

Transverse striping was seen to occur on all the basic colors distinguished except beige. For the basic colors from white to dark brownish red, the secondary color was almost exclusively black. For the basic color dark brown, the secondary color was light brown. For the basic color black, both reddish beige and white secondary colors were seen.

Spots may vary greatly in number and size. Usually larger spots are present in low numbers, while tiny spots frequently occur in large numbers. Spots are usually distributed irregularly in the ruff and head tufts, although in the case of numerous tiny spots in the ruff, they frequently are concentrated in the upper front part. Spots may occur in one or two secondary colors. Among the 29 males on Schiermonnikoog, 9 cases had spots in only one secondary color, and 3 cases had spots in two secondary colors. Except for one case, spots occurred exclusively on a basic color of either black or white. On a basic color of white, the secondary colors were dark, while on a basic color of black, the secondary colors were light.

At least one case among the 200 plumages noted had a ruff with transverse stripes (basic color black, secondary color white) and in addition some large spots in the same secondary color.

A bib may differ greatly in size. In an underdeveloped nuptial plumage a bib forms only a small area under the chin; in a fully developed nuptial plumage, however, bib feathers are long and cover the lower ruff feathers almost completely. Thus, in a fully developed plumage, the feathers of a bib are visually the most conspicuous. For this reason the color of a bib has consistently been called the basic color of the ruff and the color(s) of the non-bib feathers the secondary colors, even when the plumage was still underdeveloped. The color of the bib was plain white in all cases found in the different areas studied. A bib has been found only in ruffs in which the non-bib feathers are either plain or striped, and not on non-bib feathers with spots. The basic color of the non-bib feathers is limited to dark brownish red, yellowish brown, or white.

TABLE 7

FREQUENCY OF OCCURRENCE OF CONTRAST IN PATTERN BETWEEN RUFF AND HEAD TUFTS AMONG MALES ON SCHIERMONNIKOOG IN 1960 AND 1961

Pattern in head tufts	Pattern in ruff				
	Plain	Spotted	Striped	Bib	Striped + Bib
Plain	5	6	1	2	0
Spotted	4	3	1	0	0
Striped	0	0	6	0	1

(3) *Contrast between ruff and head tufts*

A contrast may exist between ruff and head tufts in both color and pattern. Ruff and head tufts will be said to be in harmony when they match in basic color, secondary color(s), and pattern. In all the cases observed in the different areas, there was at least partial harmony between ruff and head tufts. That is to say, contrasting ruff and head tufts agree in at least one color—frequently the basic color of the head tufts matches a secondary color in the ruff—or in pattern (or lack of pattern). The contrasts observed in the plumages of the 29 males on Schiermonnikoog are presented in Table 7. It can be calculated from the table that 14 of the males show harmony of pattern, while 15 show contrast. Contrast in color is shown by 3 of the 14 males showing harmony in pattern; all 3 belong to the group with plain ruff and head tufts.

(4) *Color of the wattles*

The wattles occur in different shades of yellow and red. The various shades distinguished and the frequency of each among the 29 males on Schiermonnikoog are presented in Table 8. On Schiermonnikoog, wattles showed yellow hues more frequently than red hues.

TABLE 8

FREQUENCY OF OCCURRENCE OF COLOR OF WATTLES DISTINGUISHED AMONG MALES ON SCHIERMONNIKOOG IN 1960 AND 1961

Color of wattles	Number of males
Yellow	16
Orange-yellow	3
Greenish-yellow	0
Grayish-yellow	2
Total yellow	21
Red	6
Orange-red	2
Total red	8

TABLE 9

RELATION OF PLUMAGE COLOR AND COLOR OF WATTLES

Predominant hue in plumage	Color of wattles	
	Yellow	Red
Reddish	4	0
Red and yellow (orange and brown)	2	2
Yellowish	7	3
No hue (black and white)	8	3

In order to investigate the relation between the color in the feathers and the color of the wattles, the plumages have been divided into groups according to color, and each group has been subdivided into those with yellow-hued wattles and those with red-hued wattles in Table 9. It can be seen from this table that among the males on Schiermonnikoog a correlation between color in feathers and wattles appears not to exist.

With this survey of the dimensions in which plumage can vary and the values each dimension can assume, it is possible to see what an immense individual diversity exists among the males. However, it not infrequently occurs that individuals with the same values on all dimensions are seen, both in the plumages of males within one area and in different areas. Without taking the color of wattles into account, among the 29 males on Schiermonnikoog three different plumage types were represented 4, 3, and 2 times each, respectively.

The first type had striped ruff and tufts with the basic color dark brown and the secondary color beige (3 of the 4 had yellow-hued wattles). The second type had plain white ruff and tufts (2 of the 3 had yellow-hued wattles). The third type had a spotted ruff and plain tufts; the basic color of the ruff was black and had light red and white spots; the basic color of the head tufts was dark brownish red; both birds of this type had yellow-hued wattles.

Thus, 23 different plumage types could be distinguished among the 29 males on Schiermonnikoog. Of the 23 different types, several have also been noted in the other three areas studied: 6 of the 23 types occurred in 4 areas, 3 of the 23 in 3 areas, 7 of the 23 in 2 areas, and the remaining 7 occurred only on Schiermonnikoog. GOETHE (1953) has stressed the fact of this repetition of certain types of plumages with respect to colors, color combinations and patterns, and has pointed to the genetical implications of this phenomenon.

In studies on the plumage diversity among male Ruffs, NAUMAN, SHARPE (both cited by KIRKMAN & OXON 1910), LINDEMANN (1951), and

GOETHE (1953) divided individual plumages into different types. All four authors used slightly different criteria so that the types of plumages distinguished by them are not identical. In Chapter III, I will present a division into types based on both differences in plumage and behavior.

Colors and pattern in the feathers of the ruff and head tufts and the color in the wattles are exactly the same in an individual male year after year. This has been proved first by males kept in confinement for several years in succession (by several different people including me), second by banded males recaptured on the lek in successive years by ANDERSEN (1948) and by VAN DEN BERG (personal comm.), and third by my own field observations of individually recognizable males in subsequent years. Thus, these differences between males in color and pattern of the feathers of ruff and head tufts and the color of the wattles are due to genetic differences. FORD (1945) and HUXLEY (1955) mention the plumage diversity in the male Ruff as an example of balanced polymorphism.

III. SOCIAL ORGANIZATION OF THE LEK COMMUNITY

A. THE LEK SITE

A typical lek site shows a number of bare spots scattered over a limited area of ground. The spots are about 30 cm across. The distances between them vary from lek to lek. On the large leks the spots are closer together on the average than on the small leks. On the large leks the distances between the centers of the spots measured about 1 meter, on the small leks they measured about 1.5 meters. Grass has completely disappeared from the spots which are frequently hollow, and defecation marks betray the usual presence of birds on them. Around the area with bare spots and also between them the grass is shorter than in the surrounding meadows.

Observation from a hide reveals that the bare spots on the lek are each occupied by a single male who stays there more or less continuously. It is clear that lack of grass and the hollow shape of the bare spots are caused by the trampling feet of the occupants. The spots I have called the residences of these males and the space between the residences the interresidential area. Activity takes place mainly on the residences and to a less extent in the interresidential area (see Fig. 18, 19 and 20).

B. BEHAVIOR WITHIN THE MALE COMMUNITY: INDEPENDENT MALES AND SATELLITE MALES

Two groups of males can be distinguished: independent males and satellite males. Independent males can be further subdivided into resident

males and marginal males. This classification is based upon two criteria that are normally highly correlated: (1) differences in territoriality and attachment to the lek; and (2) differences in behavior patterns that serve communication among the birds. These two criteria for distinguishing among males will each be discussed.

BANCKE and MEESENBURG (1952, 1958) distinguish three groups of males: owners, whites, and guests. These groups correspond to my resident, satellite and marginal males, respectively. Their distinctions are based upon differences in territoriality and attachment to the lek, but not, however, upon differences in behavior patterns. They focused their attention on the interactions of owners and guests, and give little information on the role the whites play in the male community.

SELOUS (1906, 1907) did not distinguish different groups of males, but describes a few cases of male behavior easily recognizable as an interaction between a resident and a satellite male (1906, p. 420; 1907, p. 171, 177-178, 367). Neither PORTIELJE (1931), LINDEMANN (1951), nor MILDENBERGER (1953) noted a behaviorally distinct group of satellite males, though it seems likely from MILDENBERGER's account that satellite males were absent in the small population he observed (cf. Section I.C.).

1. *Territoriality and attachment to the lek*

a. *Independent males*

(1) *Resident males.* Each individual residence has its own individually recognizable occupant or owner who normally stays there when present on the lek and defends it from other independent males, and who returns there after periods of absence from the lek. Males that possess their own residence I have called resident males. This means that among resident males a typical territorial situation in which neighbors defend common borderlines (cf. HOWARD 1964) does not exist. The residences themselves are defended, but the interresidential area is not specifically claimed by any of the resident males. Information presented above shows that the size of the residences is not density dependent, whereas the size of the interresidential areas is dependent on the number of residences on a lek.

The amount of time spent on the lek by resident males changes gradually during the season with an optimum in the middle when courtship is at its peak. In the beginning and end of the season the time spent on the lek is rather confined to a period in the early morning and to a less degree in the afternoon. In the optimal period of the season most resident males are present nearly continuously during the day. They leave only after the morning activity to make short foraging trips in the neighborhood of the lek (cf. BANCKE and MEESENBURG 1952). As soon as one of the males on the lek shows any reaction to conspecifics approach-

ing the lek, however, all the resident males hurry back to their residences.

Resident males start occupying the lek before dawn while it is still completely dark. They arrive singly or a few at a time usually within a short time of each other.

Resident males visit a neighboring lek only exceptionally; on the other lek they always have the status of marginal male (see Fig. 19).

Occasionally, after violent fighting, a resident male loses his residence to another male. Such a loser usually leaves the lek and returns only in the status of marginal male (cf. Section III.B.2.a.2).

(2) *Marginal males.* When present, marginal males are located at the margin of the lek, outside the residences. They stay at a slightly greater distance from the residences than the average distance between residences on the lek, although they sometimes place themselves on an unoccupied residence at the outer edge of the lek. Marginal males are present on the lek only irregularly. They usually arrive in the company of satellite males and females. In general, marginal males do not stay long at the lek, but fly off soon after their arrival. Frequently they are driven away by the resident males nearest them. Males that lose their residence on a lek and drop down in status to marginal male visit the leks even less frequently than other marginal males.

Marginal males start visiting the lek only after sunrise when courtship is at its peak.

Marginal males visit more than one lek, though often a preference for a particular lek may be shown. The more frequent the visits of a marginal male to a particular lek, the stronger his preference is for a special location at the edge of the lek. The more often a marginal male is present, the greater is the chance that he will not be driven away by nearby resident males. Apparently the resident males become accustomed to the presence of such a marginal male. In this way a marginal male may gradually attain a more stable position. It is then possible that such a marginal male gradually diminishes the distance between his usual spot and the nearby residences; he may finally be able to maintain himself on his spot when attacked by a resident male. At this point such a male may be said to raise in status from marginal male to resident male (cf. Section III. B.2.b.2.).

Since marginal males are potential possessors of residences and resident males may drop in status to marginal males after losing their residence in a fight, the status between resident males and marginal males is apparently interchangeable. For this reason I have combined them into the group of independent males.

The differences between resident males and marginal males can be considered as differences in rank. They differ from each other in their success in defending a residence at a particular location on the lek. Thus, one can conceive of resident males as being equal in rank among each other, but higher in rank than marginal males.

The observations of BANCKE and MEESENBURG (1952, 1958) on owners and guests are in complete agreement with my observations. Their owners have a "run" (residence) on the "hill" (lek) and defend their run from other owners. Guests stay at the border of the hill and are not tolerated by owners. An important difference between our observations will be discussed in Section III. B.2.a.2.

b. *Satellite males*

A behavioral contrast to the group of independent males is shown by satellite males. These males play a completely different role in the lek community. Their behavior never leads to the acquisition of their own residence. Rather, a satellite male makes use of the residences of the resident males and stays together with the possessor on his residence. In their interactions with resident males, satellite males do not show any form of overt aggressive behavior.

The reaction of a resident male toward a visiting satellite male shows great variation. On the one hand, a resident male may allow the satellite male to enter his residence and to remain there with him. On the other hand, a resident male may try to expel the satellite male by attacking him.

A satellite male does not visit one specific resident male exclusively although he tends to show a preference for one or two particular resident males; but in general a satellite male behaves very opportunistically and, depending on the situation on the lek, frequently changes hosts. When females are visiting the lek, satellite males usually try to enter a residence where females are standing nearby; during periods without females, they normally stay on or near the residence of their usual host.

Two or more satellite males may visit the same residence simultaneously. Overt aggressive behavior is never shown between such satellite males.

On the lek RW (Schier. 1960), 4 of the 6 resident males were usual hosts, each for one special satellite male. When all four satellite males came to visit the lek at the same time, they were distributed over different residences. In contrast, on lek AH (Schier. 1960) one of the 5 resident males was the preferred host by several satellite males. Frequently two or three satellite males were present at the same time and stayed there together on his residence with him.

It is possible to distinguish between central satellite males and peripheral satellite males. Unlike the subdivision of the independent males, however, the differences between satellite males are much less sharp. Central satellite males visit the residences and the area between the residences more frequently and for longer periods than peripheral satellite males; further, peripheral satellite males tend to retreat to the margin of the lek. Central satellite males are also much more tolerated by the resident males than are the peripheral satellite males.

Thus, central satellite males show some correspondance to resident males in that they spend most of their time in the central area of the lek; similarly, peripheral satellite males correspond to marginal males in that they spend much (small lek) or most (large lek) of their time in the peripheral areas of the lek.

On the large leks, satellite males are fiercely attacked by the resident males as soon as they enter the space in between the residences and try to enter one. Both central and peripheral satellite males are attacked. Only the central satellite males are able to maintain themselves there for a short period and only a few of the central satellite males succeed in settling down on a residence. The owners of these residences are somewhat more tolerant than other resident males. On the small leks resident males do normally not attack satellite males when they enter the space in between the residences and all satellite males are accepted as guests on the residences. After they have settled down, however, the owner of the residence may start to attack the visiting satellite male. Peripheral satellite males are more readily attacked by resident males than central satellite males.

In conclusion, the degree of toleration of resident males toward satellite males varies from lek to lek: on the small leks the toleration is generally higher than on the large leks. On a particular lek, the toleration may vary among the individual resident males and depends also on the individual satellite males.

The total amount of time spent by individual satellite males on the lek is strongly affected by the toleration of the resident males and varies greatly from lek to lek. At the one extreme, one satellite male on a small lek spent nearly as much time on the lek as the resident males; at the other extreme peripheral satellite males visited the lek only infrequently and for short periods especially at the large leks.

In the morning, satellite males start visiting the lek after the resident males have arrived, at about the same time as the females.

Satellite males visit different leks, though some show a strong attach-

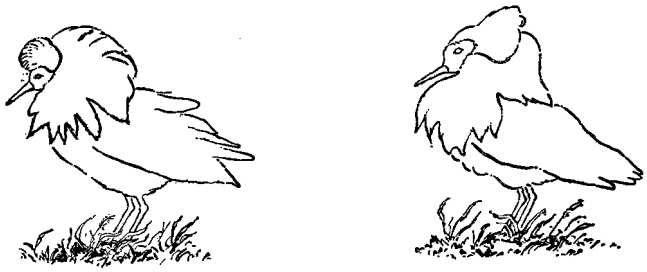


FIGURE 2. Normal oblique posture. *Left*: resident male. *Right*: satellite male.

ment to only one lek. Satellite males visit leks frequently in the company of marginal males and females. It is often observed that such a mixed group flies from one lek to another.

Transformations from satellite male to independent male or vice versa have never been observed. This is true both within a single season and between successive seasons. This rule, however, applies only to behavior considered in the long run. It may very occasionally occur that a male shows behavior that contains features characteristic of another group. Such anomalous behavior was shown by only a few marginal males and by a few pronounced central satellite males. Anomalous behavior is discussed in more detail in the section on behavior patterns.

The differences between independent males and satellite males cannot be interpreted in terms of rank. Independent males are concerned with establishing and defending a residence, while satellite males are not. A satellite male merely makes use of a residence in the company of the owner, but shows no tendency to conquer the residence from the owner. One can conceive a satellite male to be either a parasite or symbiont of the resident male with respect to the residence depending on the advantages or disadvantages of the host-guest relationship for the resident male. Possible advantages of the host-guest relationship for the resident male will be suggested later in Section III.D.5.c.

The information given by BANCKE and MEESENBURG on satellite males is mainly confined to the following remarks: that satellite males are "not bound to a decided run on the hill"; that they do not "take part in the attacks of the owners against the guests"; that they differ from the guests in that they have "free access to the hill"; and that the satellite males visit a neighboring lek on which they also acted "in the way characteristic for whites". These observations are in complete agreement with mine. However, a description of the behavior of satellite males with

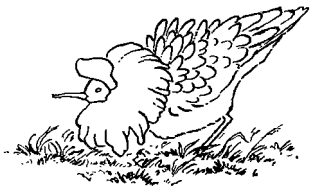


FIGURE 3. Hidden-tail forward. Resident male with bill pointing forward, directed toward an opponent.

respect to the residences of the resident males and of their interactions in the male community is not presented.

2. *Behavior patterns*

The purpose of this section and the later section on behavior patterns with females present on the lek is to describe briefly the behavior patterns shown by the birds, and to indicate the typical situations on the lek in which these patterns occur. Detailed descriptions of the form of the individual behavior patterns will be given in Chapter IV.

Behavior shown when only resident males are present on the lek will be described first, followed by behavior shown when both resident males and marginal males are present, and finally behavior when both independent and satellite males are present. In each situation all behavior shown in previous situations is still seen, but new patterns are added.

a. *Resident males only on the lek*

(1) *Periods without mutual encounters.* During great parts of the day, the lek is populated only by resident males. This situation is usually a period of reduced activity in which the resident males remain quietly on their residences and do not show any behavior directed toward each other. Rather, sleeping attitudes, comfort activities, and a display posture called the normal oblique posture (Fig. 2, left male and Fig. 8, left male) are shown. (See for the detailed descriptions of oblique postures Section IV.A.3.) In these postures the males do not orient with respect to each other; usually they face into the wind. During such periods without mutual encounters, the interrelations among resident males are stable: changes in residences were never observed.

On rare occasions the birds on the lek fly off one after the other. This behavior is usually caused by disturbances from outside the lek, but

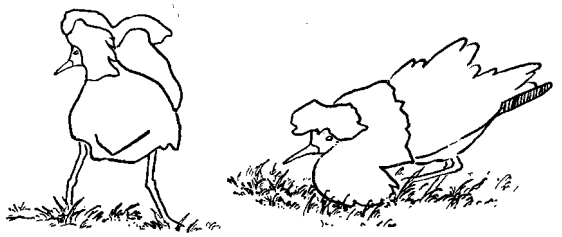


FIGURE 4. Agonistic encounter between two resident males each standing on his residence. *Left*: turning away from opponent in normal oblique posture. *Right*: turning toward opponent in ordinary forward combined with bill thrusting toward the ground.

sometimes birds fly off to follow after a group of conspecifics that leaves the lek or passes by. Certain resident males tend to stay on the lek even when most of the others have left. If three or fewer males remain, they show two alert postures in succession: first they adopt the cone upright posture that gradually changes over into the sleeked upright posture (Fig. 5 and 6). These postures differ in degree of sleeking the feathers of the ruff and head tufts. After adopting the sleeked upright, these remaining males fly away, unless other resident males return in the meantime; they then change back to the cone upright and soon show the behavior typical for a lek with normal occupation. (See for the detailed descriptions of upright postures Section IV.A.4.)

(2) *Mutual encounters*. Once in a while a period of reduced activity is interrupted by a short period during which mutual encounters occur between males. At this time resident males show mutual display while standing on their residences, or they leave their residences in order to approach and fight with each other. Immediately after such behavior, each male returns to his own residence.

During mutual encounters resident males may show the following behavior patterns directed toward one another: fighting, attack, smash, charge, chasing, three forward postures (Fig. 3, Fig. 4, right male and Fig. 9, left male) which may be combined with bill thrusting and/or tail trembling, and the normal oblique posture combined with bill thrusting. These behavior patterns, although clearly of different complexity and with some overlap, have been chosen because they are convenient descriptive units in distinguishing among the different types of males.

Fighting consists of a series of attacking acts interspersed with

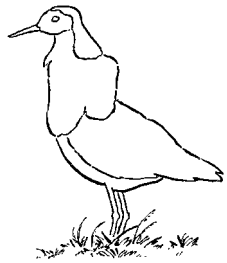


FIGURE 5. Marginal male in cone upright. This posture may be assumed by a resident male.

FIGURE 6. Marginal male in sleeked upright. This posture may be assumed by a resident or satellite male.

defensive acts which are directed away from the opponent. (See for the detailed descriptions of the attacking and defensive acts Section IV.A.1.) Attacking acts include pecking, jumping, kicking, grappling with feet and bill, feather pulling and wing beating, which is done with both wings at the same time; these elements can be combined in different ways and occur in different orientations. Defensive acts will be described later. At least three typical patterns or methods of attacking may be distinguished. First, the attacker delivers successive pecks at his opponent's head while facing him; the pecks are directed toward the wattles on the face. Second, the attacker jumps from a frontal position toward the chest of the opponent and kicks him, or grapples and pulls his feathers with toes and bill; this is combined with wing beating. Third, the attacker jumps on top of his opponent, and while standing on his back, grapples and pulls his feathers with toes and bill; this is also combined with wing beating. In the less vigorous fights only the first method is seen. In fights of greater vigor both the second and third methods are seen. The third method is the most forceful and is most likely to be continued for a longer time. The two opponents both try to use the second and third methods of fighting with the frequent result that neither bird can complete the sequence: in many cases both birds jump at each other simultaneously and then fall down. Fights vary in length from a few seconds to several minutes. Fighting usually takes place in the area between the residences, though sometimes it actually occurs on a residence.

The attack, the charge, and chasing are all locomotory patterns per-

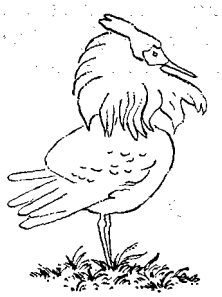


FIGURE 7. Marginal male in head-back posture with the neck slightly stretched.

formed in one of the three forward postures; in the attack the locomotion is followed by one or more attacking acts, usually a peck or a jump toward the opponent. An attack leads to fighting if the attacked bird returns the attack. Frequently, however, a male immediately returns to his residence after attacking, before a counterattack takes place. The charge differs from the attack in that the locomotion is not followed by an attacking act. Instead, the charging male returns before he has reached the opponent. During chasing a male runs after a fleeing bird. In form, chasing is identical to charging.

The smash is a form of attack in which the male swoops down from the air and kicks and/or pecks the opponent. The smash occurs regularly when a returning resident male finds another independent male on his residence.

The forward postures and the normal oblique posture with bill thrusting are normally performed while standing on the residence. Three forward postures may be distinguished: the hidden-tail forward (Fig. 3) which is shown exclusively in the short period about dawn; the ordinary forward (Fig. 4, right male and Fig. 9, left male) which is shown during the rest of the day; during severe territorial fighting a losing male shows the low forward toward the end of the fight just before he quits. In the beginning of the fight he shows one of the other two forward postures like other resident males involved in the fighting. (See for the detailed descriptions of the forward postures Section IV.A.2.)

During mutual encounters resident males may show the following behavior patterns directed away from one another: defensive acts during

FIGURES 8, 9 and 10 are successive stages of the behavior of a resident male on his residence (*left*) and a satellite male standing somewhat outside the residence (*right*).

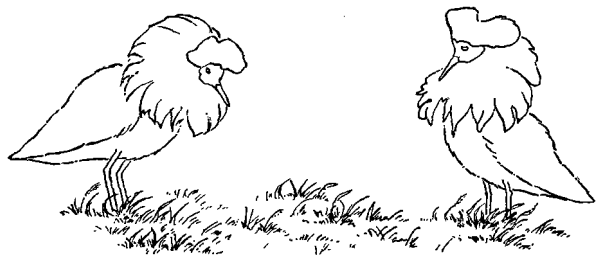


FIGURE 8. Resident male in normal oblique posture in a front-side orientation with respect to the satellite male; satellite male in normal oblique posture facing the resident male.

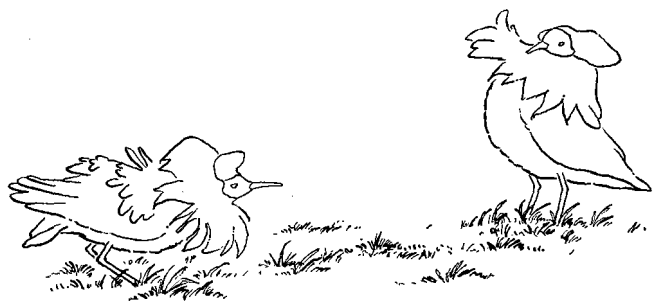


FIGURE 9. Resident male in ordinary forward thrusting his bill toward another resident male on the lek (not shown); satellite male head jerking in reaction to the bill thrusting resident male.

FIGURE 10. Resident male in oblique posture with nearly perpendicular bill and head turned away from satellite male; satellite male in oblique posture with the ruff in the circle posture and head turned away from resident male.

FIGURE 11. Satellite male in circle tiptoe with bill obliquely downward.

FIGURE 12. Satellite male in circle tiptoe with perpendicular bill.

fighting, bill thrusting towards the ground while facing the opponent (Fig. 4, right male), turning away (Fig. 4, left male) sometimes combined with bill thrusting toward the ground, the head jerk, and returning to the residence. The defensive acts include head turning toward the side while in a frontal orientation, head turning toward the ground while the opponent is on his back, pulling the head back (with the bill still pointing forward) while facing the opponent, and shaking the opponent from his back. These defensive acts could only be distinguished properly in slow motion film. When turning away and bill thrusting toward the ground are combined, they are performed in the hidden-tail or ordinary forward or in the normal oblique posture. The head jerk is given only in the normal oblique posture in reaction to a neighboring resident male that abruptly approaches his residence through the air. Returning to the residence is done in the hidden-tail or ordinary forward postures.

Within the male community resident males show agonistic behavior toward each other rather infrequently during the day, and then only in short bouts. The usual inducement for a mutual encounter is locomotion of a resident male in the interresidential area. At the very moment that such a male passes by another one's residence the owner may adopt an agonistic display posture directed toward the moving male, or he may charge or attack. Also the return of a resident male which has been temporarily absent from the lek easily induces an agonistic encounter between resident males. Normally such an encounter involves only two males. Turning away combined with bill thrusting toward the ground shown simultaneously by the two males is the usual way an encounter ends. An encounter usually stops soon after it has started. An example will be given to illustrate a typical sequence of behavior.

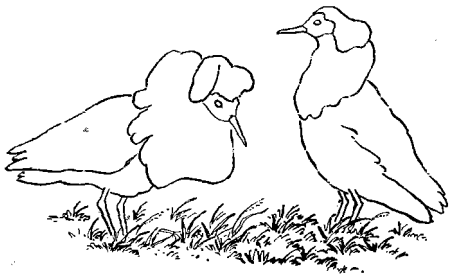


FIGURE 13. Resident male (*left*) and satellite male (*right*) together on a residence. The resident male is in the normal oblique posture in a front-side orientation with respect to the satellite male; satellite male is in the sleeked upright almost facing the resident male.

Resident male A is standing on his residence in the normal oblique posture. Resident male B is returning to the lek through the air. On noticing B, A starts bill thrusting in the normal oblique posture directed toward the approaching B. When B is about to land, A changes to bill thrusting in the ordinary forward. The bill thrusting of A is followed by the smash in B. Immediately after the smash, B lands and runs to his own residence in the forward. A then attacks B with a peck, but returns immediately to his residence in the forward without further fighting. Both birds then turn away from each other and bill thrust toward the ground in the forward posture. Finally both males adopt the normal oblique posture.

The short period of the resident males' arrival at dawn, however, is characterized by continuous interactions in which all the resident males take part. Bill thrusting toward each other or toward the ground while facing the opponent or while turning on the residence is displayed for a much longer time than in a similar situation later in the day. Also characteristic of the dawn period is that bill thrusting toward the ground sometimes leads to actual pecking into the ground, which almost never occurs during the day. Moreover, the displays are performed exclusively in the hidden-tail forward, while later in the day the ordinary forward is used in similar circumstances. Finally, the frequency of charge and attack are somewhat higher than during agonistic encounters later in the day, especially on some leks in the beginning of the season. Part of this increase in agonistic behavior can be explained by the fact that the resident males are returning to their residences early in the morning and are thus moving outside their residences. However, the encounters tend to last much longer than under similar circumstances later in the day, which

suggests that each male may, in a sense, have to re-establish his residence each day.

When females are also present on the lek, the frequency of displays, charges, attacks, and fighting among resident males is much higher. Agonistic behavior on a lek with females present is discussed in detail in a later section.

All the agonistic behavior among resident males described above generally leads to stabilized interrelations among the resident males.

Occasional changes in the occupation of the residences, however, do occur. In the three years of observations, 7 cases have been noted in which a resident male lost the ownership of his residence. In 6 of these 7 cases, the resident male returned to the lek in the status of marginal male; in the seventh case the male was never seen again and was probably the male found dead a few days later. In 4 of the 6 cases, the resident male was driven away only after severe territorial fighting; in most of the cases several resident males took part in the fighting in succession; in one of the 4 cases, the original owner succeeded reconquering his lost residence from the new possessor a few days later. In another of the 4 cases the loser of the fight established himself on the original residence of the conqueror shortly after the fight, and thus acquired the status of resident male again; in this particular case it was a matter of an exchange of residences between two resident males, although the conqueror was a former marginal male that shortly before had gradually established a residence (see Fig. 19). In 2 of the 6 cases, the loss of ownership did not occur in my presence, but was very likely similar to the cases I did observe since one of the males was involved in severe territorial fighting in the days preceding his drop in status.

Such severe territorial fighting may last up to about 10 minutes. Afterwards the males involved are clearly exhausted: they pant heavily with their bills open for several minutes. Sometimes the males wound each other; the relatively tender bill is easily damaged, and lumps on the bill are normally caused by fighting. On one occasion a male was bleeding severely after a very serious fight that he finally lost.

An external inducement for such severe territorial fighting does not seem to be present. All of a sudden one male takes the initiative and attacks.

Two of the 4 territorial fights I observed involved males who returned unusually late in the early morning, well after the other males had arrived. The other two cases took place later in the morning. Four of the 6

changeovers probably due to territorial fighting happened in the beginning of the season, the other two happened toward the end of the season.

In general, agonistic behavior among males serves residence defense and leads to stabilized interrelations among the owners of the residences, whereas severe and prolonged fights are used to bring about changes in the occupation of the residences on the lek.

These data contrast rather strongly with the data of BANCKE and MEESENBURG (1958), who studied one lek one day a week for 10 weeks. Their lek, in my terminology, would be considered a small lek with the number of resident males varying between 3 and 8. During their observations they saw 6 changeovers, 2 early in the season and 4 in the end of the season; changeovers occurred considerably less frequently during the course of my observations. The 4 cases they observed at the end of the season involved males that shortly before still had the status of marginal male; this was true of 1 of the 6 cases I observed. Further, their data show that 10 marginal males were able to establish a residence at the edge of their lek (or were in the process of doing so), whereas during my three years of observation only three cases of a marginal male establishing a residence on a lek were seen. Although they do not mention the exact number of marginal males that visited the lek, some of their data show that this number is relatively much higher than on the leks I observed. Presumably, the relatively high number of marginal males on their lek caused a strong pressure for the establishment and conquest of residences, whereas such pressures were not very strong on the leks I observed. These pressures may be related to the changing size of the population and the size of the leks within the population.

b. *Resident males and marginal males on the lek*

(1) *Marginal males landing on the lek.* The most usual posture adopted by marginal males at the margin of the lek is the cone upright (Fig. 5). With sleeking of the feathers of the ruff and head tufts, this posture may gradually change over into the sleeked upright (Fig. 6). These two upright postures are identical in form to the two alert postures shown by resident males on a lek that is only partially occupied. In these postures a marginal male nearly never faces the lek. A less usual posture is the head-back posture (Fig. 7), which may be considered a variety of the normal oblique posture. In this posture the marginal male is usually oriented with his side toward the lek. The head-back posture is shown especially by marginal males that have the status of resident male at a neighboring lek.

A marginal male that lands on an unoccupied residence may adopt the normal oblique posture or the ordinary forward sometimes combined with bill thrusting. These behavior patterns do not differ in form from

the corresponding ones in resident males. In these postures a marginal male may have an orientation toward the lek.

(2) *Interactions between resident males and marginal males.* Resident males in general show the following behavior toward marginal males: attack, charge, or chase; or, while standing on their residence, bill thrusting in the ordinary forward or normal oblique posture. When attacked, marginal males do not normally return the attack, but immediately fly away; when charged, they either take off or run away in one of the two upright postures mentioned above. Thus, fighting between resident males and marginal males is normally not seen. A resident male may continue to chase a fleeing marginal male until it flies away. Marginal males show a variable reaction to bill thrusting of a resident male: a marginal male in one of the upright postures usually flies away; a marginal male in the head-back posture usually shows the head jerk, but remains where he is; a marginal male standing on a residence in the normal oblique posture or ordinary forward may bill thrust in return, though this usually evokes an immediate attack from the resident male, and the marginal male then normally leaves the lek.

A marginal male that is in the process of establishing his own residence on the lek (cf. Section III.B.1.a) usually adopts the normal oblique posture. A male in this posture seldom evokes an attack from a neighboring resident male. If such a marginal male resists flying away during the rarely occuring attack from a resident male, and remains on his regular spot, the marginal male is then considered to have risen in status to resident male. Normally, no fighting ensues in such a case because the former marginal male usually does not counterattack, and the resident male usually returns to his residence after performing the first attacking act. This lack of fighting is in contrast to the severe territorial fighting associated with the conquest of an occupied residence among resident males.

(3) *Interactions among marginal males.* Marginal males, when present on the lek at the same time, usually stand widely spaced at the margin of the lek. Marginal males that do meet at close distances may, however, ignore each other. Rather infrequently marginal males interact with each other. In that case they show behavior patterns identical to the ones shown in the mutual encounters among resident males. Even attack and fighting may be shown on occasion.

c. *Independent males and satellite males on the lek*

(1) *Interactions between resident males and satellite males.* First, the inter-

actions between a resident male and a satellite male together on a residence will be considered. A satellite male may arrive on a residence either directly from the air or by walking or running toward the residence over the ground. From the time of arrival there are four general ways of interacting between a resident male and a satellite male, which depend on the size of the lek and on the status of the satellite male. Interactions between a resident male and a central satellite male or a peripheral satellite male on a small lek and on a large lek will each be described in turn.

On a small lek, after arrival on a residence, a central satellite male adopts the normal oblique posture (Fig. 2, right male and Fig. 8, right male). This posture in the satellite male (Fig. 2 and 8) differs from that of the resident male in that the resident male holds his bill in a conspicuous way in front of his body while the satellite holds his head somewhat back in such a way that his bill is partially concealed in his ruff. The resident male may react to this behavior by adopting the squat posture (cf. Fig. 16, right male), a horizontal posture in which the bill is pressed vertically to the ground, and head and bill are turned away from the satellite. (See for the detailed descriptions of horizontal postures Section IV.A.5.) The satellite male in the normal oblique posture normally faces the squatting resident male. The resident usually freezes in the squat posture for several seconds or longer. He then gradually stretches his legs, while his body stays in a horizontal position with his bill still perpendicular to the ground. This attitude is called the half-squat. From the half-squat, the resident male gradually changes to an oblique posture with the bill still perpendicular to the ground, and finally he adopts the normal oblique posture. Both males are then standing in their normal oblique posture (Fig. 8); the resident male usually has a sideward orientation to the satellite male, while the satellite male may face the resident male. Frequently both males hold the head turned away from the other (Fig. 10). One or more stages of the above sequence in the behavior of the resident may be left out. In the extreme case, the resident male stays in the normal oblique posture after arrival of the satellite male and only turns his head away. This latter reaction by a resident male is more likely to occur when the satellite arrives by walking over the lek. (See Diagram 1.A.)

A resident male and a central satellite male may stay together on the residence for a prolonged period of time, both remaining in the normal oblique posture; the satellite male sometimes stands a few steps away from the residence. Occasionally the resident male may show bill thrusting toward the satellite male or even actual head pecking. The vigor and

DIAGRAM 1

TYPICAL BEHAVIOR SEQUENCES WHEN A SATELLITE MALE ARRIVES ON A RESIDENCE ON A LEK WITHOUT FEMALES
(n.o.p. = normal oblique posture; ± means: with or without)

A. *Arrival of a central satellite male on a small lek.*

R: n.o.p. → squat → half-squat → o.p. with perpendicular bill → n.o.p. ± bill thrusting, ± head pecking → n.o.p.

S: n.o.p. ——————————————→ n.o.p. ± head jerk, ± head turning → n.o.p.
→ tiptoe ——————→ n.o.p.

B. *Arrival of a peripheral satellite male on a small lek.*

R: n.o.p. → squat → spread-tail forward ± turning, ± bill thrusting, ± head pecking → half-squat → o.p. with perpendicular bill → n.o.p.

S: squat → flees from residence
n.o.p. with perpendicular bill → tiptoe ± perpendicular bill → sleeked upright → leaves residence
± head turned away

C. *Arrival of a central satellite male on a large lek.*

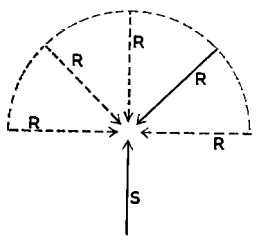
R: n.o.p. → squat → spread-tail forward ± turning, ± bill thrusting, ± head pecking, ± feather pulling, ± wing beating → squat

S: squat
squat → flees from residence

frequency of both movements are usually low. The satellite male reacts to these movements either with a head jerk from the normal oblique posture and/or by turning his head away sidewards from the resident male, or by adopting for a short time an upright posture with the bill pointing further downward and with the ruff first in the circle posture, immediately changing into the fan posture; these upright postures are called the circle and fan tiptoe respectively. As the result of these ruff postures the bill becomes less conspicuous.(See for the circle tiptoe Fig. 11 and 12). A satellite male may also jerk and/or turn his head away when the resident male thrusts his bill at another resident male which is situated in the general direction of the satellite male (Fig. 8, 9 and 10). (See Diagram 1. A.)

On a small lek, after arrival on a residence, a peripheral satellite male adopts the squat posture. The resident male then squats with him forming a twosome and usually places his bill vertically on top of the head of the satellite male, at the same place the bill is placed during copulation. The most usual orientations of the resident male and the satellite male squatting together in a twosome with respect to each other are shown in Diagram 2. Other positions also occur.

DIAGRAM 2



Both males may freeze in this position for some time. The resident male may intersperse squatting with other behavior shown toward the visiting satellite male. He then raises himself slightly and adopts the spread-tail forward (cf. Fig. 16). In this posture he may turn from side to side around the head of the satellite male who remains in the squat. Standing in the spread-tail forward, the resident male may also show bill thrusting or head pecking toward the squatting satellite male. The pecks are delivered with the bill held either in a horizontal or vertical position. After performing such behavior the resident male squats again placing his bill again on top of the satellite male's head. In this situation it has never

been observed that the satellite male attacks in return. Usually a satellite male endures such treatment from the resident male, although repeated head pecking may drive the satellite male off. He then retreats to the edge of the lek where he adopts an upright posture with the bill held horizontally and the feathers of the ruff and head tufts more or less sleeked; based on the degree of sleeking the feathers, two successive stages in such an upright posture are distinguished: the sleeked-front upright and the sleeked upright; the last posture does not differ in form from the corresponding posture in resident males and marginal males.

In the case that the peripheral satellite male is not driven away from the residence, both males end the squat after some time. The resident male then shows the same sequence of activities described above for the resident male who is visited by a central satellite male. The satellite male ending the squat is likely to adopt the following three postures in succession: the normal oblique posture, the circle and fan tiptoe, all three with the bill turned down and/or the head turned away from the resident male. The tiptoe postures of the satellite male may be followed by the upright postures as described for the satellite male at the edge of the lek. Soon after adopting the sleeked upright while either standing at the edge of the lek or still on the residence, the satellite male usually flies away (Fig. 13). Normally a peripheral satellite male does not stay on a residence for a prolonged period of time; he is either driven away by the resident male or leaves of his own choice. In the presence of females on the lek, a peripheral satellite male be somewhat more persistent in continuing the squat posture. (see Diagram 1.B.)

On a large lek, a central satellite male squats on arrival at the residence as quickly as possible. On most residences, however, the resident male immediately attacks the satellite male severly showing head pecking, feather pulling, and wing beating; the satellite male normally flees from such a residence. On a few residences, however, the resident male squats with the satellite male and acts like a resident male on a small lek toward a peripheral satellite, although he sometimes shows the more severe attacking acts like grappling in combination with feather pulling and wing beating. Wing beating is performed while standing on top of the satellite male's back. If not driven away by the resident male's attacks, the central satellite male may stay on the lek for a prolonged period of time, continuing the squat posture. The resident male may also continue the squat posture. (See Diagram 1.C.)

On a large lek, a peripheral satellite male rarely succeeds entering and squatting on a residence. The resident male behaves toward the

peripheral satellite male in the same way as toward the central satellite male, but the peripheral satellite male is much less able to endure such treatment and is easily driven away by the resident male. Thus, on a large lek, a peripheral satellite male stays on a residence only infrequently and for a short period of time.

Second, the interactions between a resident male on his residence and a satellite male outside the residence will be considered. In this situation also there are different ways of interacting between a resident male and a satellite male, mainly depending on the size of the lek.

Satellite males move around in the interresidential area in order to choose or change hosts. In this area they move in the tiptoe postures: on large leks only the circle tiptoe (Fig. 11 and 12) is seen, while on small leks both the circle and fan tiptoe are seen. On a small lek, a satellite male in the tiptoe is normally not attacked, whereas severe attacks regularly occur on large leks. On a small lek, a satellite male moves around in this area quietly, deliberately choosing his host; on a large lek a satellite male runs quickly, trying to avoid the attacks of the resident males and chooses a residence in a hurry. As soon as a satellite male has entered a residence, he need only endure the attacks from his host; attacks from a resident male on a neighboring residence have been observed very rarely and exclusively on large leks. On a small lek, a peripheral satellite male may leave a residence and retreat to the edge of the lek where he adopts an upright posture as described above. This posture may evoke a charge or attack from a resident male; the satellite male usually reacts by flying away from the lek.

(2) *Interactions between marginal males and satellite males.* Encounters between marginal males and satellite males do not normally occur on a lek with males only present.

(3) *Interactions among satellite males.* Mutual encounters among satellite males occur only when two or more satellite males visit the same residence at the same time. In oblique or upright postures, satellite males tend to ignore each other. When satellite males squat together with the resident male forming a threesome, foursome, etc., however, they normally hold their heads close to each other, most times actually touching each other. The resident male holds his bill on top of the head of one of the satellite males, always the one with the most pronounced peripheral status.

d. *Anomalous behavior of independent males and satellite males*

As mentioned above (Section III.B.1.b), on rare occasions a male may

show uncharacteristic behavior. Among the independent males, three marginal males have been observed to show such anomalous behavior: 2 of 19 independent males on Schiermonnikoog and 1 of 40 independent males in the Oosterwolde Polder. One of these males showed an underdeveloped plumage characteristic of young males; the other two had fully developed plumage. One of these two, however, had a crumpled leg and the other showed anomalous behavior only early in the season before he became a resident male on another lek.

Anomalous behavior among independent males is characterized by the following features. The marginal male approches a residence while it is occupied by the resident male. During the approach the marginal male adopts a horizontal posture with the bill slightly turned toward the ground with the feathers of ruff and head tufts only partially raised; this posture is different from the one shown by a resident male or a satellite male when approaching a residence occupied by its owner. The marginal male approaches the residence slowly and pauses from time to time; during a pause a sideward orientation toward the resident male is usually adopted. After arrival on the residence, the marginal male squats. The resident male sometimes squats with him and freezes for a short while forming a twosome. When both males raise themselves from the squat to turn from side to side, the marginal male adopts a forward posture with the bill pointing forward but with the ruff and head tufts only partially raised; thus this posture is different from the spread-tail forward which the resident male adopts at the same time. Either during the approach or, more usually, when the marginal male adopts the peculiar forward posture the resident male attacks him; the marginal male then flees immediately. It should be noted that the behavior patterns of the marginal males in these situations are typical neither of independent males nor of satellite males, but are rather intermediate.

The two males from the population on Schiermonnikoog that showed anomalous behavior both approached the same resident male most of the time. This particular resident male was also the preferred host of several satellite males.

Among satellite males, behavior characteristic of independent males has been observed only among pronounced central satellite males. This behavior was seen in 3 birds: 2 of 8 satellite males on Schiermonnikoog and 1 of 29 satellite males in Hasselt. The following cases have been noted. First, anomalous behavior was shown toward a resident male: two satellite males showed attack and fighting with the owner of the residence adjoining that of their usual host on a total of five occasions. Second,

anomalous behavior was shown toward a marginal male with an underdeveloped nuptial plumage: attack and fighting were seen twice, once outside the residences and once on the residence of a resident male which was temporarily absent; mutual pecking while standing outside the residences was seen once; a charge only was seen twice. Third, anomalous behavior was shown toward a peripheral satellite male: on six occasions a satellite male showed head pecking toward the peripheral satellite male while it was squatting on the residence of the preferred host; on two of these occasions this behavior succeeded in driving the peripheral satellite male away. Fourth, anomalous behavior was shown toward a marginal male performing anomalous behavior; the satellite male once charged when the marginal male approached the residence occupied by the satellite male and his host.

The behavior patterns shown by satellite males in these situations do not differ in form from the corresponding behavior patterns shown by independent males. It is possible to consider these examples as a sort of residence defense or host defense.

3. *Survey of behavior patterns and interpretations*

A brief survey of the most important behavior patterns shown by males on the lek is given in Table 10. This table indicates in a general way the frequency of occurrence of these patterns in the different groups of males; it also indicates toward which other birds these patterns are shown.

The arrangement of the activities in this table is based primarily on similarity in form. The hypothesis underlying this arrangement is that behavior patterns with similar form will, in many cases, also be similar in motivation. The proper analysis of how far similarity in form is due to homology (including similar causation) or convergency in each specific case must be left for later investigations.

Except for the attacking acts, the various behaviour patterns have been grouped according to the orientation of the body axis. The forward postures are characterized by a body axis that varies from oblique downward to horizontal, and by a forward pointing bill. The oblique, upright, and horizontal postures are characterized by a body axis that is oblique upward, vertical, and horizontal, respectively; the horizontal postures are further characterized by a downward pointing bill.

Apart from the horizontal postures, that form a special case, and the attacking acts, the order of the groups in the table is also based on similarity in form. Each group will be discussed briefly.

Attacking acts. These acts are basically a functional group: the various patterns all involve forceful bodily contact with, and serve to repel, another bird. In this table, however, they are grouped together on the assumption that, in this case, common function goes hand in hand with common motivation. This assumption is supported by the facts that these behavior patterns occur together under similar external circumstances, they are preceded by locomotion directed toward the opponent, and they are normally shown only toward other males. It is further assumed that the group of attacking acts corresponds to the highest level of activation of the behavior mechanisms causing attack. If the hypothesis that similar form implies similar motivation is true, it then follows that the other groups of behavior patterns (except for the horizontal postures) are arranged according to decreasing activation of the behavior mechanisms causing attack. In the following, to avoid cumbersome language, the terms aggression and aggressive motivation will be used to denote these behavior mechanisms and their state of activation, respectively.

Forward postures. These behavior patterns, except for the up-tail forward, are normally directed toward another male and are frequently combined with bill thrusting. A forward posture is assumed preceding and during the charge and attack; and adoption of a forward posture, particularly when combined with bill thrusting often leads another male to attack. These postures are therefore considered to express predominantly aggressive motivation.

Oblique postures. These behavior patterns have no characteristic orientation with respect to other birds. On some occasions, however, (e.g., when combined with bill thrusting) they are directed toward another male, and on other occasions (e.g., when combined with a head jerk) they are directed away from another male. In form, these postures are intermediate between the aggressive forward postures and the escape upright postures (see below). Thus, on the basis of both orientation and form, these postures are considered to express balanced agonistic motivation.

Upright postures. These behavior patterns are very different in form from the attacking acts, but are all similar in form to the posture a bird assumes just prior to flying up (cf. DAANJE 1950). Further, some of these postures immediately precede flying up. Thus, whereas aggressive motivation is predominantly absent, these postures are all considered to be at least partially controlled by the causal mechanisms for flying up. The cone upright and the sleeked upright are also considered to be escape postures: these patterns are almost always directed away from another

TABLE 10

BEHAVIOR PATTERNS SHOWN BY MALES ON THE LEK

Shown by:	Resident male				Marginal male			Satellite male		
With respect to:	R	M	S	♀	R	M	♀	R	S	♀
Attacking acts										
Wing beating	+	—	±	—	—	(+)	—	—	—	—
Feather pulling	+	—	±	—	—	(+)	—	—	—	—
Grappling	+	—	±	—	—	(+)	—	—	—	—
Kicking	+	+	—	—	—	(+)	—	—	—	—
Jumping	+	—	±	—	—	(+)	—	—	—	—
Pecking	+	+	+	—	—	(+)	—	—	—	—
Forward postures										
Hidden-tail forward	+	—	—	—	—	—	—	—	—	—
Spread-tail forward	+	+	+	—	—	—	—	—	—	—
+ Bill thrusting	+	+	+	—	(+)	(+)	—	—	—	—
Up-tail forward	—	—	—	+	—	—	—	—	—	—
Low forward	+	—	—	—	—	—	—	—	—	—
Oblique postures										
Normal oblique posture	+	+	∓	—	(+)	—	—	∓	—	—
+ Bill thrusting	+	+	∓	—	(+)	—	—	—	—	—
+ Head jerk	+	—	—	—	(+)	—	—	∓	—	—
Oblique posture with perpendicular bill	—	—	∓	—	—	—	—	∓	—	—
Head-back posture	—	—	—	—	+	—	—	—	—	—
+ Head jerk	—	—	—	—	+	—	—	—	—	—
Low-wing posture	—	—	—	+	—	—	—	—	—	—
+ wing lifting	—	—	—	+	—	—	—	—	—	—
Strutting	—	—	—	—	—	—	—	—	—	+
Upright postures										
Wing fluttering and flutter jumping	—	—	—	+	—	—	+	—	—	+
Puffed upright	—	—	—	+	—	—	—	—	—	—
Tiptoe	—	—	—	—	—	—	—	+	—	+
Cone upright	—*	—	—	—	+	—	—	—	—	—
Sleeked upright	—*	—	—	—	+	—	—	+	—	—
Horizontal postures										
Squat	—	—	+	+	—	—	(+)	+	—	+
Half-squat	—	—	∓	—	—	—	—	—	—	—
Low horizontal	—	—	+	+	—	—	(+)	∓	—	+

R = resident males
M = marginal males
S = satellite males

\+ = occurs normally
(+) = occurs infrequently
— = does not occur normally

In cells where two signs are given, the upper sign refers to behavior shown on a large lek, the lower sign to behavior shown on a small lek. Signs in all columns except with respect to females refer to the occurrence of behavior on the lek when no females are present. Occurrence of behavior patterns in the presence of females will be discussed in section III.D.2. Patterns marked with an * are shown by resident males on a lek when disturbed from outside the lek.

bird or predator. The other behavior patterns included among the upright postures probably have a more complicated motivation.

Horizontal postures. The squat shows great similarity in form to the copulatory posture, and is frequently shown with respect to females. Thus, it is considered to be at least partially controlled by the causal mechanisms underlying copulation. The squat, however, is frequently shown by resident males and satellite males toward each other when females are not present, which suggests that this posture may also be influenced by other mechanisms. The squat shows marked similarities in form to the posture shown by a nesting female after she has been flushed from her nest by a potential predator such as man: she crouches at some distance from the nest. Two components are clearly recognizable in the form of this crouched posture: one to stay and one to escape. It seems likely that the mechanisms underlying these components will also contribute to the control of the similarly shaped squat. Further, the squat of the resident male contains an aggressive component in that his bill is placed on top of the head of the squatting satellite male. Aggressive motivation is also suggested by the fact that the resident male frequently alternates the squat with the spread-tail forward combined with bill thrusting or head pecking toward the satellite male; the satellite male alternates the squat with the non-aggressive low horizontal. It seems very likely that aggression is more predominant in resident males than in satellite males. These facts suggest that as well as copulatory motivation, the squat may express the influence of behavior mechanisms to stay, to escape, and to attack.

The half-squat appears to be a transition between the squat and the normal oblique posture and is presumably controlled by causal factors common to both postures.

If these hypotheses about the motivation of the various behavior patterns are accepted, several conclusions about the motivational balance within each category of male emerge from Table 10. These conclusions are discussed first among independent males, second between independent males and satellite males, and third among satellite males.

Among resident males, behavior is shown which is either predominantly aggressive or shows balanced agonistic motivation. Toward marginal males, resident males show the same behavior as they do toward other resident males, but the marginal males react with behavior in which escape is very marked. Among marginal males, interactions usually do not occur, but if they do occur, behavior similar to that shown among resident males is seen.

Between resident males and satellite males, on large leks, resident males show behavior that is predominantly aggressive, while on small leks, resident males show behavior with relatively balanced agonistic motivation toward satellite males. Only toward peripheral satellite males do they sometimes show predominantly aggressive behavior. Toward resident males, on a large lek, satellite males show primarily behavior in which aggressive motivation is predominantly absent, but in which a moderate escape motivation is present; while on a small lek the central satellite males frequently show behavior in which both aggressive and escape motivation is very weak. Encounters between marginal males and satellite males do not occur in the male community and are therefore not included in the table.

Among satellite males, although satellite males encounter one another on the residences, the absence of mutual interactions suggests that they do not stimulate the activation of aggression and escape in each other.

On the basis of what has been said above, it can be concluded that on the lek resident males have a strong aggressive motivation (and stronger on large leks than on small leks), but only a weak escape motivation, and that marginal males have a weak aggressive motivation, but a strong escape motivation. The motivation of the satellite males is clearly well balanced with respect to aggression and escape, but there is some question whether the absolute level of activation of these behavior mechanism is high or low. There are two main arguments to support the contention that both aggression and escape are only weakly activated in satellite males. First, more actual attack and escape should be seen among satellite males if aggression and escape were highly activated, since fluctuations in both behavior mechanisms must occur, and there is no reason to expect that these fluctuations would always precisely balance each other. Second, resident males on small leks presumably show behavior with relatively agonistic motivation toward satellite males, and the behavior of marginal males that are in the process of becoming resident males presumably reflects relatively balanced agonistic motivation at some point in the process; yet in neither of these cases do independent males show behavior typical of satellite males. On the other hand, on those occasions when satellite males do show either escape (young satellite males) or attack (older satellite males with optimal plumage that sometimes show anomalous behavior), the intensity or vigor of these behaviors is comparable to the vigor of escape and attack behavior among independent males. It is possible that the reason overt attack and escape are seen so rarely among satellite males is that the relatively high

sexual motivation of satellite males stabilizes the interaction of aggression and escape in the sense of KRUIJT (1964: 148 ff.). In any case, it is clear that further study of this problem would be necessary in order to come to a firm conclusion about the absolute level of aggression and escape in satellite males.

Resident males and marginal males appear to be essentially the same with respect to their available repertoire of behavior patterns; the differences between the two groups can be explained in terms of rank. Satellite males seem to be essentially different from the independent males with respect to their repertoire of behavior patterns, presumably because of the belance and/or absolute levels of aggression and escape. These differences in the internal state explain why the different groups of males react in different ways to the same stimulus situation. The satellite behavior patterns in which both aggression and escape components are predominantly absent evidently have a strong attack-inhibiting or appeasing effect on the resident males. By means of such behavior patterns the satellite males succeed in settling down on a residence with the owner present.

These conclusions about differences among groups of males based upon differences in behavior patterns completely confirm the identical distinction based upon territoriality and attachment to the lek.

4. *Factors influencing the status of independent males and satellite males*

a. *Independent males*

In general, resident males have a fully developed plumage, and are thus older males (cf. Section II.B). Only two examples of resident males with slightly underdeveloped plumage have been noted: one male on lek AH on Schiermonnikoog in 1960 rose to resident status at the very end of the season; one male on the north lek in Roderwolde in 1962 had resident status during the entire observation period. These two males were presumably younger than the average resident male.

Marginal males consist of different groups of males. First there are the males which have a resident status on other leks. The only resident males that visit other leks are those which do not have a very stable resident status. On Schiermonnikoog in 1960, in the period that the two leks existed, it was very exceptional that any of the resident males visited the other lek, whereas before the formation of lek RW, the 6 future resident males of that lek were regularly seen on lek AH in the status of marginal males. Of the 6 marginal males distinguished on the north

lek in Roderwolde, two had the status of resident male on the south lek. In the Oosterwolde Polder, 4 of the 13 marginal males distinguished on the large lek had the status of resident male on the small lek, whereas of the 13 marginal males on the small lek, none was a resident male from the large lek. This shows that the resident males on the large lek had a greater attachment to their lek than the resident males on the small lek. Also in Hasselt in 1962 only resident males from the two smaller leks visited the large lek in the status of marginal male while the resident males on the large lek remained there.

Second, a part of the marginal males consists of males with underdeveloped plumage: thus, young males. The work of VAN OORDT and JUNGE (1934) suggests that an underdeveloped nuptial plumage is caused by a low level of testes hormone in the blood. On Schiermonnikoog in 1960, 3 of the 9 marginal males had an underdeveloped plumage. In 1962 a new marginal male with an underdeveloped plumage appeared. Marginal males with an underdeveloped nuptial plumage also occurred on leks in the other areas.

Third are the marginal males that have a fully developed plumage, but which do not have resident status on another lek. The occurrence of such males can be certain only among the males on Schiermonnikoog where I was sure to know all the existing leks (assuming, at least, that these males did not have a resident status on other leks outside the island). In the other areas studied, other leks did occur at distances of more than 1 kilometer at which I did not observe. At least three categories of males are included in this third group: (1) marginal males that rose to resident status in subsequent years; (2) older males that have been forced off their residence during interterritorial fights; and (3) independent males with an anomalous nuptial plumage (see Section III.C.).

This survey suggests that the status of an independent male normally changes through his lifetime in such a way that he begins in the status of marginal male, with increasing age he acquires the status of resident male, and still later in life loses his resident status and becomes a marginal male again. Independent males with an anomalous plumage, however, are evidently at a disadvantage and are not as likely to acquire resident status. The observations of a few resident males which had partially underdeveloped nuptial plumage, and of some marginal males with plumage characteristic for independent males which had fully developed plumage show that individual differences occur with respect to the timing of the normal cycle.

b. *Satellite males*

In general, central satellite males have a fully developed plumage, although on the small leks on Schiermonnikoog, one satellite male with slightly underdeveloped plumage was able to maintain himself very well on the residences. Thus, central satellite males are generally older birds.

Peripheral satellite males consist of two groups. First is the group of males with underdeveloped nuptial plumage, probably caused by low hormone level (see above). An extreme example of this group was found on Schiermonnikoog in 1960 where a male with very short nuptial feathers and a complete lack of wattles visited the lek and residences. The time spent on the residences was minimal. Only in the year after his wattles started to develop did this male rise slightly in status. Thus, younger satellite males generally have a peripheral status.

The second group of peripheral satellite males consist of males with anomalous plumage. The effect of anomalous plumage on the status of satellite males is discussed in Section III.C.

These observations suggest that satellite males change their status from peripheral to central as they grow older in a manner parallel to the change in status of independent males. I did not find any indication, however, that at a still later age a satellite male reassumes his peripheral status again. Satellite males with an anomalous plumage, similarly to independent males, appear to have a reduced chance of acquiring central status.

5. *Frequencies of males of different status*

The frequencies of males of different status in the different observation areas are presented in Table 11. A male has been categorized as a resident male if he had that status for one or more days on the lek during the total observation period; this categorization does not imply that he had resident status continuously.

In 1960, two leks, AH and RW, existed on Schiermonnikoog. Lek RW, however, existed only until May 17. From that time on the resident males of lek RW were seen only irregularly, either as marginal males at lek AH or in the neighborhood of either the discontinued lek RW or the former lek mentioned in section I.C. From 1961 on, the situation was rather peculiar in that the lek RW was not reestablished again. Instead, the former resident males on that lek and some of the marginal males established small, temporary leks, frequently changing location. The number of resident males on them varied from one to three, and none of them had a very stable resident status. The frequency of visits by

TABLE 11

FREQUENCIES OF MALES IN THE DIFFERENT GROUPS

Area	Year	Lek	Absolute numbers					Percentage	
			R	M	I	S	Total	I	S
Schier.	1960	AH	5	9	20	7	27	74%	26%
		RW	6						
	1961	AH	5	7	18	6	24	75%	25%
		tl	6						
	1962	AH	3	7	15	3	18	83%	17%
		tl	5						
	1963	?	?	?	11	2	13	85%	15%
Roder.	1962	SL	12	6	24	16	40	60%	40%
		NL	6						
Hasselt	1961	Large	15	14	29	16	45	58%	42%
		Small	unobserved						
	1962	Main	15						
		Sec	6	16	42	30	72	58%	42%
		Small	5						
O.P.	1962	Large	19	16	43	27	70	61%	39%
		Small	8						

R = resident males I = independent males
M = marginal males S = satellite males

satellite males and females on the temporary leks was low compared with the frequency on lek AH.

The occupation by resident males on the south lek in Roderwolde was rather unstable.

In Hasselt, two leks existed in 1961. These were located at two opposite ends of a small lake: the large lek and the small lek. In 1961, observations were made only at the large lek. In 1962, the large lek was split up into two separate leks at a distance of about 50 meters from each other: the main lek and the secondary lek. The small lek was reestablished at the same location. During the course of the 1962 season, the number of resident males on the main lek diminished gradually.

It should be realized that the exchange between resident males and marginal males makes it rather arbitrary in specific cases in which group a particular male is placed. I have consistently assigned the males according to the status in which they spent the majority of the observational days.

The data in Table 11 show that the proportions of independent males and satellite males vary remarkably little between the areas Roderwolde, Hasselt, and the Oosterwolde Polder, whereas on Schiermonnikoog the proportion of independent males is relatively higher, and increases in

TABLE 12

NUMBER OF MALES RETURNING TO SCHIERMONNIKOOG IN SUCCESSIVE YEARS

Males first seen in:	Year of observation							
	1960		1961		1962		1963	
	I	S	I	S	I	S	I	S
1960	20	7	17	5	13	3	10	1
1961	—	—	1	1	1	0	0	0
1962	—	—	—	—	2	0	0	0
1963	—	—	—	—	—	—	1	1
Total	20	7	18	6	16	3	11	2

I = independent males S = satellite males

successive years as the total number of males on the island decreases.

Table 12 shows the number of males on Schiermonnikoog that returned in successive years. These data show the overall decline in the size of population during the four years of observation. They also suggest that the rate of decline for satellite males is greater than for independent males. The number of birds is too small to accept this last conclusion with much confidence, but, if true, it might indicate that resident males have a greater tendency to return to the usual breeding grounds and leks than satellite males under unfavorable conditions.

C. PLUMAGE AND ITS CORRELATION WITH BEHAVIOR IN INDEPENDENT MALES AND SATELLITE MALES

During observations on the lek it is easy to see that the differences in behavior between independent males and satellite males are associated with differences in the nuptial plumage. During the lek observations, I got the impression that males with dark or colored ruff and head tufts were predominantly independent males, while nearly all satellite males seemed to have white or predominantly white ruff and head tufts. It further seemed to me that males with white ruff and black head tufts and males with black ruff and white head tufts belonged to the independent males. I could nearly always predict which status a male had on a lek on the basis of the color of the ruff and head tufts: there were only a few particular types that were either independent male or satellite male. Such types were found on leks in different areas. They occurred among the males with colored ruff and head tufts and among the males with a black or dark gray pattern in the white ruff and tufts.

BANCKE & MEESENBURG (1952) mention that they distinguished three satellite males and that these three were all characterized by a white ruff, fair ear tufts and, on the whole, light feathers; they further mention that no males with white ruffs were seen among the marginal males. These remarks and their term whites which is used to denote the group of satellite males (1952 and 1958) indicate that these observers were also aware of the correlation between behavior and plumage. Their observations, hower, were still incomplete and, therefore, only partially true since the correlation is much more complicated than their observations suggested.

A survey of the plumage diversity within both groups of males is presented in Table 13. The color of the ruff and tufts separately is used to divide the birds into different categories which are arranged according to brightness of the plumage. The actual categories of color were chosen in such a way as to separate independent males from satellite males most clearly. This survey includes all the males for which the necessary information was available. Males that visited more than one lek in an area are counted only once. Some errors may be made in this respect because the large number of very similar white or nearly white satellite males that visited both the large lek and the small lek in the Oosterwolde Polder and in Hasselt were difficult to distinguish individually in the relatively short period I spent at these leks.

The most obvious conclusion to be drawn from the data in Table 13, as seen in the totals in the bottom row and the last column, is that the proportion of independent males decreases while the proportion of satellite males increases as the plumage changes from dark to light. If the data are looked at more closely, it is seen that the three categories of black head tufts (first column), black ruff (top row), and dark colored ruff and head tufts (second group of second row) contain 86% of the 132 independent males and only 7% of the 82 satellite males. In the most of the remaining groups the satellite males outnumber the independent males; 93% of the satellite males and only 14% of the independent males are found in these groups.

The group with light colored ruff and head tufts apparently forms a transitional stage between the common independent pluamge and the common satellite plumage.

The group with white ruff and head tufts both with a pattern causes the only disruption in the gradual change in proportion between independent males and satellite males within rows or columns. The disruption is most obvious when we compare this group with the groups in the two pre-

ceding columns. A detailed inspection of the plumages in this group shows that all 11 independent males have a black or dark gray transverse striping in the ruff and head tufts, while only 3 of the 9 satellite males have such a pattern, and one of these very weakly; the remaining 6 satellite males have a white bib on a striped plumage or only a few spots in the white plumage. Thus, on the average, the amount of black (or dark gray) in independent males is greater than in satellite males of this group. Thus, even within this group, the differences between independent males and satellite males can be correlated with difference in the brightness of ruff and head tufts.

We may conclude that independent males are strongly associated with a dark color in ruff and head tufts and satellite males are strongly associated with a light color in ruff and head tufts. The typical plumage of independent males has black or dark-colored ruff and head tufts or a white (or almost white) ruff with black head tufts. The typical plumage of satellite males has a white or almost white ruff and head tufts or, somewhat less common, a white or almost white ruff with colored head tufts.

The term anomalous has been used to denote plumages which are typical for males of the opposite group. Satellite males with black or dark-colored ruff and dark-colored tufts have, for instance, been considered as satellite males with anomalous plumage; independent males with white ruff and tufts both with a black or dark gray striping have been considered as independent males with anomalous plumage.

On Schiermonnikoog, 3 independent males had anomalous plumage. The one with the least pronounced anomalous plumage (a white bib on yellow and black lower ruff feathers, and yellow tufts) had the status of resident male on the lek RW in 1960, but before and after the existence of this lek in 1960, and in 1961-1963, this male was frequently present on the third display site where a lek existed in former years as mentioned in section I.C., or he acted as a marginal male on lek AH. The other two independent males had a more pronounced anomalous plumage. One was of type *J* (white ruff and tufts both with a black transverse striping) and the other of type *N* (white ruff and yellow head tufts). These two males had the status of resident male only for a short period in the beginning of the season on lek AH, and both lost their residence in severe territorial fighting with other resident males before courtship and mating had reached their seasonal optimum. From that time on, both males kept the status of marginal male in the remaining part of the season and in the one year after that when they were present. Thus the two independent males with the most pronounced anomalous plumage

TABLE 13

OCCURRENCE OF INDEPENDENT MALES (I) AND SATELLITE MALES (S) WITHIN PLUMAGE GROUPS IN THE VARIOUS AREAS

Ruff		Head tufts											
		Black		Dark color		Light color		White, pattern		White, plain		Total	
		I	S	I	S	I	S	I	S	I	S	I	S
Black	Schier.	7	0	2	1	0	0	0	0	1	0	10	2
	Roder.	5	0	1	0	0	0	0	0	1	0	7	0
	Hasselt	12	0	4	0	0	0	1	0	0	0	17	0
	O.P.	17	0	2	2	2	0	1	0	1	0	23	1
		41	0	9	3	2	0	2	0	3	0	57	3
Dark color	Schier.	2	0	6	0	0	0	0	0	0	0	8	0
	Roder.	2	0	6	1	0	0	0	0	0	0	8	1
	Hasselt	3	0	7	2	0	0	0	0	0	0	10	2
	O.P.	7	0	3	0	0	0	0	0	0	0	10	0
		14	0	22	3	0	0	0	0	0	0	36	3
Light color	Schier.	0	0	0	0	0	0	0	0	0	0	0	0
	Roder.	0	0	0	0	1	0	0	0	0	0	1	0
	Hasselt	0	0	0	0	1	3	0	0	0	1	1	4
	O.P.	0	0	0	0	1	0	0	0	0	0	1	0
		0	0	0	0	3	3	0	0	0	1	3	4
White, pattern	Schier.	2	0	0	2	1	0	1	1	0	1	4	4
	Roder.	1	0	1	0	1	3	4	0	0	0	7	3
	Hasselt	5	0	0	2	0	4	3	5	0	1	8	12
	O.P.	3	0	0	1	0	1	3	3	0	1	6	6
		11	0	1	5	2	8	11	9	0	3	25	25
White, Plain	Schier.	0	0	0	0	1	0	0	1	0	3	1	4
	Roder.	1	0	0	0	0	2	0	4	0	6	1	12
	Hasselt	6	0	0	1	0	2	0	3	0	6	6	12
	O.P.	3	0	0	0	0	9	0	1	0	9	3	19
		10	0	0	1	1	13	0	9	0	24	11	47
Total		76	0	32	12	8	24	13	18	3	28	132	82

did not succeed in maintaining a stable resident status due to their interaction in the male community and as a result of their marginal status they were not successful in mating.

Of the 10 anomalous independent males of type *J* noted on leks in Roderwolde, Hasselt, and the Oosterwolde Polder, 7 had the status of resident male at the time of observation and 3 had the status of marginal male. Of the 3 marginal males, two had underdeveloped plumage and their status was thus probably due to their young age. It was typical for these 7 resident males that they spent less time on the lek than the average resident male, that their residences had in all cases an edge or corner

position, and that they were usually avoided as host by satellite males and did not belong to the males most preferred by the females. (cf. Section III. D.3.c).

In the different areas, five independent males of type *P* (black ruff and white or almost white tufts) were noted. Their white tufts can be considered as an anomalous feature in the plumage of independent males. A striking fact was that all these 5 males had the status of marginal male, although their plumage was fully developed and thus young age could not be responsible for their status (cf. Section III.B.3).

A contrasting example in this respect was found in an independent male with anomalous plumage on the large lek in the Oosterwolde Polder. This male had light beige (just off-white) ruff and head tufts with black lower ruff feathers and a few small black spots in the ruff. This was the resident male who reached by far the highest rate of copulation of all males on the lek (36% of the total 92 copulations).

These data suggest that in general independent males with an anomalous plumage have less chance within the male community to reach a stable resident status, but that females do not discriminate against a resident male with anomalous plumage and make their choice among the males independently of the color of their plumage, but on the basis of other external and behavioral features (cf. Section III.D.6.c).

On Schiermonnikoog, one satellite male with anomalous plumage (black ruff with red and white spots and dark brownish red tufts) was noted. His plumage was fully developed and thus he could be considered an adult male. Considering the development of his plumage, this male was less able to maintain himself on a residence than other satellite males: he acted more like a peripheral satellite male than like a central satellite male. His status obviously was due to his interactions in the male community. As a result of his peripheral status his rate of copulation was relatively low. In their choice among the doubly-occupied residences on the lek, the females appeared not to discriminate against the satellite male with an anomalous plumage. Anomalous satellite males noted on other leks provide a similar picture.

D. Behavior on the Lek with Females Present

1. *Visits of females to the lek*

Females visiting the lek land in the interresidential area. After landing, they place themselves near a residence where they usually remain until they fly away; sometimes, however, they walk from one residence to

another. Females that stand very near a residence sometimes step on the residence and crouch and copulate. Copulation usually takes place only on a residence and occurs only after the female crouches. Both resident males and satellite males may copulate; marginal males have never been observed to copulate except on one occasion (cf. Section III.D.2.g). On rare occasions, a female that has copulated on one residence afterwards walks to another residence and copulates again. Females often leave the lek without copulating or even crouching. Females may choose a residence occupied with only its owner or a residence with its owner and one or more satellite males. Certain individual males are chosen more frequently than others as copulating partners.

Females visit the lek only for short periods. They arrive singly or a few at a time, frequently in the company of satellite males and marginal males. Females start visiting the lek shortly after dawn—well after the resident males' pre-dawn arrival. The frequency of visits reaches a peak about an hour after sunrise; by mid-morning females are rarely present. During the height of the season, females also visit the lek in the afternoon (cf. BANCKE & MEESENBURG 1952).

Females may visit different leks. Females have frequently been observed to fly directly from one lek to another. It is not possible, however, to determine to what extent females visit different leks without individually marking the birds.

SELOUS (1906, 1907) was the first to observe that, during the visits of the females, males stay on their own residences and that the female makes the partner-choice; he also saw that the residences are the places "dedicated to the performance of the nuptial rite". These observations were confirmed by BANCKE and MEESENBURG (1952, 1958). These latter authors apparently did not see copulation take place between a satellite male and female.

2. *Behavior patterns*

a. *Females approaching the lek and landing or passing by*

Females normally approach the lek by air. In reaction to the approach of a female, males on the lek may show a sequence of very conspicious communal displays called the reception ceremony that takes at the most a few minutes. The reception ceremony is shown in its most complete form on small leks; on large leks the reactions of males on the lek to approaching females are much less intense. Behavior shown on small leks will be described first.

On a small lek, males that are standing in the normal oblique posture look around very attentively. They appear to have remarkable ability in

discovering flying conspecifics at great distances from the lek. A male may, for instance, react to a group of conspecifics several hundred meters away. The resident male or satellite male that sees approaching conspecifics reacts immediately with wing fluttering. Other males present on the lek immediately react to his behavior by turning and looking in the same direction. If it is not a false alarm, all the males soon join in wing fluttering facing the flying conspecifics. As the conspecifics come closer, communal wing fluttering is continued and may be followed by communal flutter jumping and hovering above the lek; all the birds on the lek continue orienting toward the flying conspecifics. It is probable that wing fluttering is released by any group of flying conspecifics at a distance, including groups of males only; flutter jumping and hovering are shown especially as a reaction to a large group including females. In all three behavior patterns the white undersides of the wings make a flashing effect that makes the birds clearly visible from afar. These displays are performed by both resident males and satellite males; the position of head and bill, and ruff and head tufts during wing fluttering and flutter jumping is slightly different in the two groups of males. Resident males perform these displays on or above their residences, while satellite males usually perform them on or above the area between the residences. Wing fluttering and flutter jumping are frequently combined with tail trembling and/or tail lifting in some individuals (Fig. 14). (See for the detailed descriptions of the behavior patterns shown during the reception ceremony section IV.A.4.)

If a group of conspecifics merely passes by, the males on the lek stop making wing movements, but remain in the upright posture identical to the posture in which they wing flutter. The postures of the resident males and satellite males show corresponding differences as during wing fluttering: resident males stand in the puffed upright; satellite males stand first in the circle tiptoe and soon pass over into the fan tiptoe. All the males continue to face the departing conspecifics. Satellite males frequently continue flutter jumping higher and higher and finally fly off to join the departing group; this behavior is seen more frequently in peripheral than in central satellite males. Resident males usually remain on the lek, although some may fly off; these are usually the resident males that spend relatively less time on the lek. All birds that remain on the lek gradually change over from upright postures to their respective normal oblique postures. (See Diagram 3.A.)

When approaching females are about to land on the lek, the males already present behave in quite a different way. Resident males, which

DIAGRAM 3

TYPICAL BEHAVIOR SEQUENCE WHEN FEMALES APPROACH A SMALL LEK BY AIR

A. *Females approach and pass by.*

R: wing fluttering → flutter jumping → hovering → puffed upright → normal oblique posture

S: wing fluttering → flutter jumping → hovering → tiptoe → normal oblique posture

B. *Females approach and land.*

R: wing fluttering → flutter jumping → hovering → up-down move. → up-tail forward → squat

S: wing fluttering → flutter jumping → hovering → tiptoe ——————→ squat

are sometimes slightly displaced after the reception ceremony, place themselves on their residences again, and while still oriented toward the approaching birds they perform up-down movements (Fig. 15, left male); particularly in certain individuals, up-down movements are combined with tail trembling, tail lifting, and/or bill thrusting. As the females land, the resident males assume the up-tail forward which is always combined with tail trembling and never with bill thrusting. In this posture resident males always face a landing female (Fig. 15, right male). When the females are actually standing on the lek, all the resident males sink into the squat and freeze in that posture on their residences; in the squat they may still face the female or, by turning just before squatting, they may adopt a side-tail orientation toward the female in such a way that they can just look at her with one eye. During the up-down movements of the resident males, satellite males move over the lek in the tiptoe (either circle or fan tiptoe) and deliberately choose their position. They walk either toward their usual host or toward a residence in the vicinity of which females are landing. Satellite males arriving with the females choose a position in a similar way. As soon as the satellite male chooses his residence, he squats, usually just before the resident male squats. Together they form a twosome in the squat. (See Diagram 3.B.)

On a large lek, the reception ceremony is much less complete and is frequently omitted altogether. In particular, hovering, flutter jumping and up-down movements are almost never seen on large leks, and wing fluttering occurs only rarely and in low intensity. Normally only the up-tail forward is shown before a resident male squats down; this behavior is shown only by resident males in the location where females land, while the others remain in or assume the normal oblique posture. Further, satellite males do not get the opportunity to move about undisturbed between the residences in order to choose their position:

resident males attack tiptoeing satellite males intensely, while satellite males on small leks are tolerated; satellite males on a large lek always adopt the circle tiptoe and never the fan tiptoe; further they always run quickly between the residences and squat on a residence as soon as possible.

If a group of conspecifics passes by, the males on the lek do not show upright postures, but merely remain or assume the normal oblique posture.

Marginal males on leks of all sizes either squat somewhere at the edge of the lek or, more usually, remain in one of the oblique or upright postures characteristic of marginal males and either stay in one place or move along the edge of the lek.

b. *Females visiting a singly-occupied residence*

A female arriving at a residence usually places herself a few steps away from it. After arrival she may assume the long-neck posture, the short-neck posture (Fig. 16), the drop-wing posture, the tail-up posture, or she may preen; she is usually oriented with her head or side toward the resident male. (See for the detailed description of female postures Section IV.B.) The long-neck posture is never continued for a long period of time, but is either followed by flying off or changes into the short-neck posture. The short-neck posture may be continued for a longer period, but if the male remains motionless in the squat, a female normally begins preening. The female sometimes changes her position by moving a few steps; such moving is often preliminary to approaching the male. An approaching female either touches the male's feathers or crouches. Feather touching occurs on the head, tufts, and back parts of the ruff. This is in the same area where a male holds a female during copulation. Males which are feather touched remain in the squat posture. Feather touching is seen mostly in the beginning of the season when females visit the lek but crouch only rarely. Females in the drop-wing posture or the tail-up posture frequently approach and crouch on the residence immediately after arrival. Crouching may also be preceded by the short-neck posture, and infrequently by preening, but never by the long-neck posture. Crouching is the actual invitation for the male to mount and copulate. In the crouched posture the female may turn with respect to the male in such a way as to either facilitate or hinder mounting. Copulation occurs after mounting.

It is frequently difficult to observe whether cloacal contact actually has taken place. In all those cases in which I observed cloacal contact

with certainty, and where it therefore was very likely that sperm transfer took place, the female showed wing flapping immediately afterwards. In contrast, many copulation attempts which were clearly unsuccessful were frequently followed by preening in the female and not by wing flapping. Therefore, for the purposes of this analysis, I have considered any copulation attempt followed by wing flapping as successful, and all others as unsuccessful. This last category was counted as copulation attempts.

When a female stands nearby, a resident male may continue squatting motionless for several minutes, sometimes for the total duration of a female's visit; a resident male in the squat usually has the side-tail orientation toward the female. (See Diagram 4.A.) A resident male may also raise himself out of the squat to perform other behavior: but, the longer a female stays at his residence, the less frequently the male interrupts his squatting. In the first place, a resident male may raise himself out of the squat into the low horizontal with his bill pointing perpendicularly toward the ground, and turn from side to side in this posture swaying his tail in front of the female; this posture is usually combined with tail trembling. The resident male normally resumes squatting again

DIAGRAM 4

TYPICAL BEHAVIOR SEQUENCES WHEN A FEMALE VISITS A RESIDENCE

A. *Singly-occupied residence.*

R: squat
squat → low horizontal posture ± turning → squat
squat → spread-tail forward { ± turning, ± bill thrusting } → squat
squat → spread-tail forward { → charge, → attack } → return → squat
squat → precopulatory posture → mount, copulate (or attempt) → squat

B. *Multiply-occupied residence.*

R: squat → spread-tail forward { ± turning, ± bill thrusting } → squat (toward males outside residence)
squat → spread-tail forward { → charge, → attack } → return → squat
squat → spread-tail forward { ± turning, ± bill thrusting, ± head pecking, ± feather pulling, ± wing beating } → squat (toward satellite males on residence)
squat → precopulatory posture → mount, copulation attempt on S → squat
squat → precopulatory posture → mount, copulate (or attempt) on ♀ → squat

S: squat → low horizontal posture ± turning → squat
squat → strutting → return → squat
squat → mount, copulation attempt on R or S → squat
squat → leaves residence in tiptoe
squat → mount, copulate (or attempt) on ♀ → squat

in a side-tail orientation with respect to the female. (See Diagram 4.A.) A resident male may also raise himself from the squat into the spread-tail forward (cf. Fig. 16); in this posture the male is usually oriented toward other males present on the lek, though on occasion he may orient toward the female. The spread-tail forward is normally combined with tail trembling and sometimes also with bill thrusting, normally directed toward other resident or marginal males on the lek; a resident male may also turn from side to side in this posture. From the spread-tail forward, a male may return to the squat, sometimes via the low horizontal, or, sometimes he may charge or attack another male. The attacked male may be a neighboring resident male which shows a spread-tail forward, with or without bill thrusting, oriented toward the attacking male. An attack may also be directed toward a marginal male or a satellite male standing or moving in the cone or sleeked upright; the attacked bird then flees. On a large lek, satellite males moving in a tiptoe and sometimes even satellite males squatting on another residence are attacked. On a small lek this happens very exceptionally. Of the satellite males' behavior repertoire, the squat is obviously the least attack provoking posture. When attacked, a tiptoeing satellite male runs quickly toward a residence to squat down as soon as possible; a squatting satellite male, when attacked by a resident male from another residence, normally continues squatting and does not flee away from the residence. After attacking or charging, the resident male returns immediately to his residence, and squats. (See Diagram 4.A.)

In reaction to a crouching female, a resident male either shows the above described behavior or adopts the precopulatory posture. (See for the detailed descriptions of this posture Section IV.A.5.) In this posture the male may turn toward the female in order to get into the position to mount. The crouching female may turn toward or away from the male to either facilitate or hinder mounting by the male. The resident male succeeds in mounting and copulating only when he and the female are roughly parallel to each other. In many cases mounting does not lead to a successful copulation because of insufficient cooperation between the two partners. After a successful copulation or copulation attempt, the resident male dismounts and immediately squats again. Frequently an unsuccessful copulation attempt is soon followed by another copulation attempt, but successful copulations may also be seen in succession. (See Diagram 4.A.) (See for detailed description of the copulation Section IV.C.) In reaction to a crouching female, the resident male on a large lek is very likely to adopt the precopulatory posture,

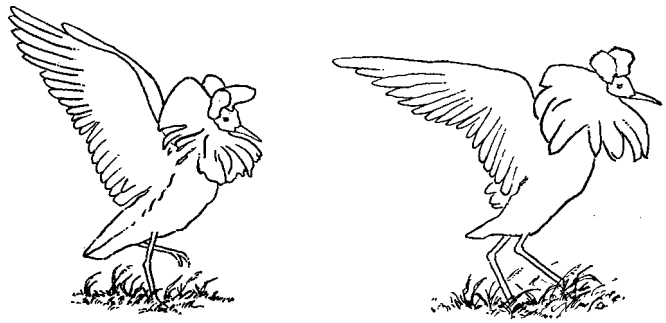


FIGURE 14. Wing fluttering. *Left*: resident male; *right*: satellite male.

mount, and copulate; the resident male on a small lek, however, is more likely to perform other behavior; even from a precopulatory posture he frequently resumes squatting before he tries to mount.

Interference during mounting or copulation occurs at a singly occupied residence infrequently. It happens when a neighboring resident male attacks the resident male or when a satellite male runs toward the couple and tries to mount also. Such interference usually prevents successful copulation.

At a singly-occupied residence on a small lek it is a rather usual occurrence that a resident male continues squatting when the female does not crouch, whereas on a large lek a resident male is more likely to intersperse squatting with other behavior independent of the female's activities.*)

A female may crouch while the male remains motionless in the squat. This is a usual occurrence on a large lek, but happens only infrequently on a small lek. On a small lek, crouching normally takes place only after the resident male interrupts squatting to perform the low horizontal or the spread-tail forward, and many of the copulations at a singly-occupied residence take place after the resident male returns to his residence from a charge or attack; at the exact moment the resident male returns to his residence, the female crouches. The frequency of the spread-tail forward and of the charge and attack on a small lek is higher the more marginal males and satellite males there are on the lek. Thus, on a small lek, the

*) It should be noted here that in this section information on singly-occupied residences on the large lek is restricted to the few which were preferentially selected by the females and were almost inaccessible for satellite males. No such information is available on the majority of singly-occupied residences on the large lek which were usually avoided by the females (cf. Section III. b. 3).

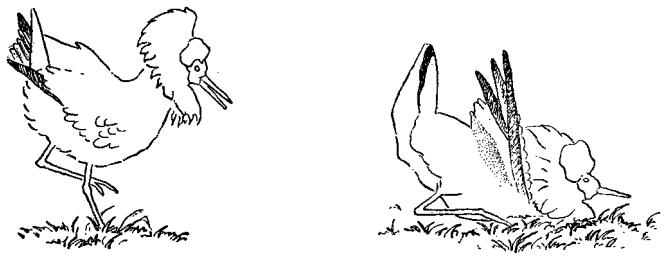


FIGURE 15. *Left*: resident male during up-down movements. *Right*: resident male in up-tail forward (After slides taken by C. J. SCHATTENKERK).

presence of marginal and satellite males increases the number of copulations that occur on singly-occupied residences.

It is possible to explain the difference in the female's behavior on a large lek from that on a small lek by considering data given below (Section III.D.5). On a large lek, a female visiting a singly-occupied residence has normally selected one of the most attractive resident males in terms of rate of copulation. On a small lek, however, a female visiting a singly-occupied residence has normally selected one of the less attractive resident males. Apparently, a female is more inclined to crouch for a squatting male if the male is one of the attractive males on the lek or, perhaps, if the male has acted as a copulating partner before.

Thus a resident male at a singly-occupied residence and a visiting female react to each other in a very different way on a small lek and a large lek. This has as a result that on a small lek the frequency of copulation at a singly-occupied residence is generally low, while on a large lek copulation at a singly-occupied residence occurs regularly.

Crouching and copulation usually take place soon after the female's arrival at the residence. When she starts preening soon after arrival, the chance that she will crouch at all at this particular residence diminishes quickly. Moreover, the longer the female continues preening during her stay, the less likely it becomes that the male on the residence will interrupt squatting to perform other behavior. In such a case the female either moves over to another residence—usually selecting one with activity, or she leaves the lek.

c. *Females visiting a residence with more than one occupant*

A female visiting a residence occupied by a resident male and one or more satellite males has the same behavior repertoire as at a residence occupied by a resident male only. Feather touching and crouching may be directed either toward the resident male or a satellite male.

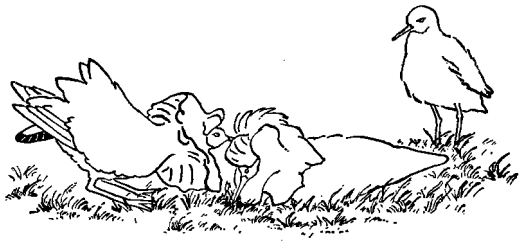
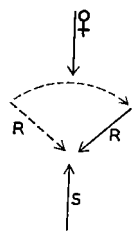


FIGURE 16. Resident male (*left*) and satellite male (*right*) together on a residence, with female nearby. The resident male is in the spread-tail forward, bill thrusting toward the satellite male; the satellite male is squatting in a side-tail orientation with respect to the female; the female is in the short-neck posture.

At a multiply-occupied residence with a female nearby, the resident male my stay on his residence and show behavior directed toward the female or the satellite male(s) on his residence or toward males outside the residence, or he may leave the residence for a short while to charge or attack other males present on the lek. A satellite male may either stay on the residence and show behavior directed mainly toward the female, or he may leave the residence and show behavior directed toward the female, change host, or take a position elsewhere on the lek.

The arrival of a female releases the squat in all males present on a residence A satellite male may also enter the residence after the female's arrival; he then squats immediately. The resident male and satellite male(s) squat together forming a twosome, threesome, etc. The resident male usually has his bill on top of the head of one of the satellite males, always the most peripheral in status. In a twosome, the resident male

DIAGRAM 5



usually adopts a side-tail orientation with respect to the female, whereas the satellite male usually faces the female. The typical orientation of a

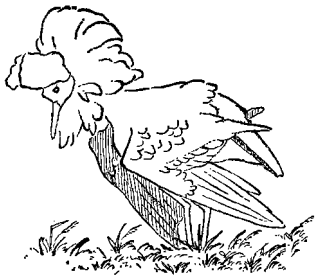


FIGURE 17. Satellite male strutting.

twosome with a female standing nearby with respect to each other is shown in Diagram 5. Satellite males usually squat with their heads touching one another.

On a multiply-occupied residence the squat is frequently interspersed with other behavior. Continuation of the squat during the total visit of the female, which occurs at a single-occupied residence on a small lek, is rare. Rising from the squat may be initiated either by the resident male or by a satellite male. As a reaction to a rising satellite male, the resident male also raises himself immediately.

A resident male with satellite males on his residence shows the low horizontal posture very infrequently, but normally raises himself from the squat into the spread-tail forward. In the spread-tail forward, he may either orient himself toward males outside the residence or toward a satellite male staying on the residence. (See Diagram 4.B.)

Toward other males on the lek, a resident male on a multiply-occupied residence shows the same behavior patterns as a resident male on a singly-occupied residence, but the frequency of such behavior is greatly increased, at least at a small lek, in the presence of one or more satellite males on the residence. Such behavior is particularly shown shortly after the arrival of a female, or when a female shows the tail-up or drop-wing postures, or when she moves (cf. Diagrams 4.A and 4.B).

Toward a visiting satellite male, a resident male shows the same behavior patterns as may be shown in the absence of a female (Fig. 16). (cf. Diagrams 1.B,C on p. 145, and 4.B on p. 168). The frequency of such behavior, especially of the more vigorous activities like feather pulling and wing beating is particularly high when the female adopts the tail-up or the drop-wing postures, or when she moves a few steps, and also when a satellite male raises himself from the squat and shows behavior directed toward the female. Wing beating, however, is shown rather

exclusively at a large lek. On a multiply-occupied residence a resident male directs such behavior toward the satellite male with the most pronounced peripheral status, whose behavior generally shows more elements of fear and is thus the most attack-provoking (cf. Section III. B.2.c.). The satellite male duffering such treatment from the resident male never attacks in return, but tries to continue squatting. Feather pulling is sometimes effective in raising him out of the squat posture, and severe head pecking and grappling in combination with feather pulling and wing beating often have the effect that the satellite male flees from the residence in a tiptoe posture and runs off either to enter another residence on the lek or to retreat toward the edge of the lek. In general, satellite males of a central status are more likely to stay on the residence and satellite males of a peripheral status are more likely to leave the residence when attacked by the resident male. (See Diagram 4.B.) Both central and peripheral satellite males, however, are more inclined to endure the attacks from the resident male and to continue squatting than when no females are present on the lek.

An additional behavior pattern shown by the resident male in the presence of a female is mounting the squatting satellite male and attempting to copulate, preceded by the precopulatory posture. The satellite male counters such an attempt either by remaining in the squat with his tail pressed to the ground, or by raising himself slightly from the squat and shaking the resident male off his back. (See Diagram 4.B.)

With a female nearby, a satellite male may continue squatting or he may intersperse squatting with other behavior. Central satellite males show a higher frequency in rising from the squat than peripheral satellite males, and in general rising occurs much more at small leks than at large leks. On a large lek, rising by a satellite male provokes immediate and vigorous attack by the resident male. On a small lek, rising may provoke attack, but does not always do so; further, if an attack occurs, it is less vigorous than on a large lek. Thus, the difference in frequency of rising by satellite males on large and small leks is likely due to learning from the experiences with resident males on the respective leks.

Unlike the resident male, the satellite male rising from the squat assumes the low horizontal posture and not the spread-tail forward; a satellite male in this posture is much lower than a resident male on a singly-occupied residence in this posture; a satellite male raises himself scarcely from the ground; further, a satellite male in the low horizontal has his tail only partially spread and tail trembling is shown only infrequently. A satellite male may turn from side to side in this posture.

During turning the satellite male usually continues facing the female in contrast to a resident male at a singly-occupied residence which orients his tail toward the female while turning in this posture. The rising of a satellite male nearly always releases the spread-tail forward and attack in the resident male as stated above. When the satellite male squats again, the resident male usually also squats forming a twosome with the satellite male. (See Diagram 4.B.)

A satellite male may also raise himself from the squat into a rather high posture—with the body axis oblique or upright—and walk slowly toward the female. This performance is called strutting (Fig. 17). It occurs mostly when the resident male has left the residence in order to charge or attack. Strutting is shown only by satellite males at small leks, particularly by central satellite males. A female usually reacts to strutting by crouching followed by retreating from the male. A copulation attempt following strutting does normally not occur. (See Diagram 4.B.)

In confinement, strutting has also been observed in independent males which do not have residences. Such males do not squat so frequently, but usually strut toward the female.

A satellite male may also try to mount and copulate with the resident male or another satellite male in the presence of a female. The mounted bird reacts to such a copulation attempt in the same way as described above. Copulation attempts on another male are seen mostly in the beginning of the season, when females are visiting the lek and residences, but crouch only rarely. (See Diagram 4.B.)

In reaction to a crouching female, a resident male on a residence with one or more satellite males usually raises from the squat immediately. He may then show the behavior patterns directed toward males outside his residence as described above. (See Diagram 4.B.) Frequently, however, the resident male raises himself into the spread-tail forward and turns from side to side hesitating between orienting toward a satellite male on his residence and toward the crouching female. In most cases he finally directs his behavior toward the satellite male, especially when the satellite male has also raised himself out of the squat and shows behavior directed toward the crouching female. In this situation the resident male and satellite male may show the same behavior patterns as when the female does not yet crouch. With a female crouching on the residence, however, the resident male is more likely to show the more vigorous attacks like severe head pecking and grappling in combination with feather pulling and wing beating, and the satellite male is more

likely to endure such treatment and not to flee from the residence. (See Diagram 4.B.)

In reaction to a crouching female, the resident male may also raise himself from the squat and adopt the precopulatory posture and try to mount and copulate with the female as described for a resident male on a singly-occupied residence. (See Diagrams 4.A. and 4.B.)

In his reaction to a crouching female, a satellite male differs strongly from the resident male: a satellite male raises from the squat and shows behavior directed exclusively to the female. A satellite male generally shows a much faster reaction to a crouching female than does a resident male. As soon as the female crouches, a satellite male may approach, mount, and copulate with remarkable speed; I have not been able to distinguish a precopulatory posture in a satellite male. In copulating itself, the satellite male also spends less time than a resident male. Further, a satellite male mounts a female as easily from a caudal position as from the side, independently of the female's facilitating turning movement. A satellite male may even succeed mounting while the crouching female turns toward the resident male. (See Diagram 4.B.)

Resident male and satellite male frequently interfere with each other during mounting and copulation. A mounting or copulating satellite male may be attacked by the resident male with head pecking and grappling in combination with feather pulling and wing beating. In some cases the satellite male still manages to copulate in spite of such an attack, but usually the satellite male then drops down from the back of the female and immediately squats again. A mounting or copulating resident male may be hindered by a satellite male because the satellite male tries to mount also, either from the side or from a caudal position. By mounting from a caudal position, the satellite male sometimes manages to push himself in between the resident male and the female. This sometimes has the effect that the resident male falls down from the female, and the satellite male and the female copulate. After an interference, the resident male and satellite male may again squat together on the residence.

Satellite males may also interfere among each other during mounting and copulation. Also among each other they do not attack, but hinder each other by trying to mount a female at the same time. This has the effect that the chance for a successful copulation by a satellite male at a residence is diminished when more than one satellite male is present at the same time. Generally, satellite males of a central status are more likely to interfere either with the resident male or a satellite male on the same residence than satellite males of a peripheral status. The latter may

continue squatting while the resident male or a satellite male copulate with a female. At a multiply-occupied residence interference most times inhibits a successful copulation. At a doubly-occupied residence, however, both resident male or satellite male may copulate successfully in the presence of the other, but a resident male succeeds more frequently just after the satellite male has been driven away from the residence, while a satellite male has a better opportunity when the resident male is temporarily absent during a charge or attack.

Interference during mounting or copulation from outside the residence occurs at the same low rate as at a singly-occupied residence, and in the same way: by the attack of a neighboring resident male or by a quickly approaching satellite male, which tries to mount also.

At a multiply-occupied residence a female may crouch, while the resident male and satellite male(s) are squatting together. But in the same way as at a singly-occupied residence, the chance that she will crouch is greatly increased when squatting is interrupted and other behavior is performed. At a large lek this happens both at a singly- and at a doubly-occupied residence. At a small lek, however, there is a marked difference in activity shown at a singly- and multiply-occupied residence: in the simultaneous presence of satellite male(s) and a female at his residence, a resident male shows an increased tendency to intersperse squatting with other behavior. Thus, at a multiply-occupied residence a female is much more stimulated to crouch than at a singly-occupied residence. The result is that at a small lek copulations are much more likely to occur at a doubly- than at a singly-occupied residence, whereas at a residence with more than one visiting satellite male interference usually inhibits successful copulation.

d. *Singly-occupied residence without females*

A resident male at a singly-occupied residence that is not approached by a female is likely to continue squatting for several minutes. He may also interrupt squatting with the low horizontal posture or with behavior directed toward other males such as the spread-tail forward, bill thrusting, charge, or attack. Such behavior is most frequently directed toward a nearby resident male that has been selected by a female. The frequency with which squatting is interrupted diminishes with the time elapsing from the female's arrival. A resident male without a female normally ends squatting while (a) female(s) are still present and assumes the half-squat, a posture in which the body axis is still horizontal but the tarsi are raised from the ground. This posture normally changes slowly into

the low-wing posture, an oblique posture with the wings hanging alongside the body. In the low-wing posture a resident male may turn from side to side, finally orienting his side toward a female on a nearby residence. During this turning he may show two-sided or one-sided wing lifted, a wing movement which momentarily exposes the male's white side. One-sided wing lifting is clearly oriented toward the distant female: normally the wing turned toward the female is lifted; the male frequently then turns 180° and lifts the opposite wing. Like the displays shown during the reception ceremony, wing lifting makes a flashing effect and is very conspicious. The male may adopt the normal oblique posture from either the half-squat or the low-wing posture. On a small lek the stages between squatting and the normal oblique posture are frequently seen; on a large lek the resident males adopt either the squat or the normal oblique posture. Many of the resident males on a large lek do not even squat if the female lands a few residences away.

e. *Multiply-occupied residences without females*

At a residence occupied by a resident male and one or more satellite males but not visited by females, the resident male and satellite male(s) squat together. Squatting may be interrupted to perform the same behavior patterns shown at a residence with females, both with respect to males outside the residence and toward each other. Mounting and copulation attempts on each other, however, do not occur as frequently. Satellite males generally endure attacks by the resident male for quite a while. Such activity frequently appears to attract a female to visit such a residence. If a female does not approach and the resident male continues his attacks, the satellite male may leave and walk over to a residence with a female. On a small lek, where satellites can move freely between the residences, changing of hosts frequently occurs; on a large lek, where moving satellites are severely attacked, a satellite male usually endures ferocious attacks from the resident male before he finally retreats to the edge of the lek.

As long as females are present at the lek, a resident male and his satellite(s) continue squatting together. Only after all females have left do they change over into the normal oblique posture. On a small lek, the satellite males change into the normal oblique posture first, followed by the resident male. On a large lek, the satellite remains in the squatted position even after the females have left. At a lek with females present, a satellite male, when entering a residence, immediately squats. On a small lek, the resident male, even when not squatting already, immediately

squats with the satellite male putting his bill on top of the satellite's head. On a large lek, the entering satellite evokes fierce attacks from the resident male. At a lek without females the squat is not necessarily shown either by resident or satellite males in the corresponding situations.

f. *Behavior of resident males outside their residence*

It sometimes happens that a resident male leaves his residence and moves closer toward a female. This is more frequently seen at small leks than at large leks. Such behavior occurs, for instance, when females preferentially visit a certain area of the lek. The resident males with residences on another area of the lek then move over toward the area visited by the females. The resident males may even reestablish a residence in such an area. On small leks, resident males may also leave their residence in order to approach females that walk from the lek.

Resident males moving outside their residences usually adopt a horizontal posture with the bill pointing obliquely toward the ground—the oblique-bill horizontal. This posture shows some similarities to both the ordinary forward and the half-squat. A resident which shows such behavior is often severely attacked by the resident male whose residence he has approached and which has been selected by the females. When a resident male stops moving he squats down and begins to act like a resident male at his own residence. He may also adopt the oblique-bill horizontal again and move closer to the female. A female sometimes approaches such a male on his temporary spot; in such a case they act together in the same way as at a residence. On a small lek, a satellite male sometimes approaches such a male while he is in the squat posture. Both males then squat together in a twosome and act like a resident male and a satellite male at a residence. Such a twosome attracts a female more often than such a resident male alone.

g. *Behavior of marginal males*

Marginal males may stay at the edge of the lek and show the same behavior as at a lek without females. This behavior is shown especially by marginal males visiting a large lek. At a small lek, marginal males may also enter a residence not occupied by its owner, where they may act like the possessor of the residence. They may also act like resident males which leave their residence in order to approach the area with females. In the presence of females, marginal males are attacked by resident males which occupy nearby residences even more severly than when females are absent. Marginal males normally do not attack resident males in return. After being attacked, they walk away toward another

area of the lek, toward the edge of the lek, or they fly off. It is unusual that marginal males in either of the situations mentioned are approached by females, although on occasion it may happen; on one occasion such a marginal male was observed to copulate.

h. *Behavior of satellite males outside residences*

As already mentioned, a satellite male may move in the interresidential area in order to choose or change hosts. The satellite male moves in a tiptoe: at a small lek either a circle or fan tiptoe is shown, while only the circle tiptoe is shown at a large lek. On a large lek, but not on small leks, such moving satellites are fiercely attacked by the resident males. On a small lek, a satellite male may also move across the lek in one of the tiptoe postures in order to approach a female which is standing on a remote part of the lek or somewhat outside the lek. When the satellite male draws near the female, he squats. Such a single satellite male in the squat is seldom approached by a female. Frequently, however, a resident male that has left his residence or a marginal male or sometimes another satellite male approaches such a singly squatting satellite and squats with him forming a twosome. If approached by a resident male or a marginal male while tiptoeing, a satellite male squats immediately and the other male joins him. A twosome appears to have a greater chance of being approached by a female than a single satellite male in the squat. Infrequently, a female may actually approach such a twosome outside the lek, but usually she walks away again quickly. Crouching or copulation do normally not occur in this situation. A satellite male frequently reacts to a female walking away by raising himself from the squat and following her in the tiptoe. The resident male then also raises himself and follows both satellite male and female in the oblique-bill horizontal. If the female stops, both resident and satellite males may again squat together. Sometimes, however, the satellite male approaches another resident male that is already squatting near the female. Thus, both a single resident male and a single satellite male in the squat posture may be approached by a satellite male and a resident male, respectively, which then squats with him and this demonstrates the attraction resident male and satellite male exert on each other even outside residences.

i. *Behavior of females among each other*

Females on the lek frequently group together near the same residence. At a large lek, even five females at one particular residence is not unusual. Although such females generally do not show behavior directed

toward each other, occasionally two females will face each other in the oblique-bill upright, an upright posture in which the bill is slightly turned downward. From this posture they may show bill thrusting directed toward each other's head; bill thrusting sometimes changes over into overt head pecking.

It has been observed that the upright posture, bill thrusting, and head pecking in this manner are also shown by adult males and juvenile birds which were kept in confinement, and which came into conflict with each other near the food and water dish or near the bathing basin. Also, juvenile birds which have not yet developed a nuptial plumage show these behavior patterns toward each other while visiting the lek.

Females standing near the same residence frequently crouch at the same time for a male on the residence. In such a situation a female occasionally mounts a crouching female and attempts to copulate. I have never observed with certainty that cloacal contact took place during such a unisexual copulation attempt. Further, I observed sexual behavior between females mostly at large leks which are visited by larger groups of females than small leks.

j. *Females leaving the lek*

Females usually leave the lek by flying off directly from a spot close by a residence. Particularly at small leks, however, they sometimes walk away from the lek just before leaving. Flying off is preceded by either a long-neck or a short-neck posture; preening also may occur at this time.

The males' reactions to leaving females is different at small leks and large leks. In general the reaction at a small lek is much stronger, in a way reminiscent of differences in the reception ceremony.

At a small lek, females which walk away are generally followed by satellite males and marginal males, and more rarely by resident males. The behavior shown by the respective males has been described above. Toward females that fly off, the males show a communal reaction in which nearly all the males take part: they rise from the squat into an upright posture and watch the females go. A resident male raises himself from the squat into the puffed upright and turns to look after the leaving females; this posture gradually changes over into the normal oblique posture. Infrequently, such a male flies after the females. Squatting satellite male(s) raise into the circle tiptoe, immediately change over into the fan tiptoe, and then slowly adopt the normal oblique posture while taking a few steps aside from the residence. Satellite males may also fly after the departing females; flying after is seen most frequently in the

more peripheral satellite males. A resident male at a multiply-occupied residence may continue squatting for about a minute if the satellite remains standing nearby, and then finally adopts the normal oblique posture. Marginal males generally join the leaving group of females.

At a large lek, there is no general communal display in reaction to departing females. The resident males that were squatting in the females' presence, raise into the normal oblique posture as the females leave and show arbitrary orientation. A few satellite males may remain at the lek and these continue squatting. The other satellite males and the marginal males follow the departing females. Such a group of females, satellite males, and marginal males is often seen to fly over and land again at a nearby lek.

3. *Differences between Small and Large Leks*

Small leks differ markedly from large leks in a number of respects that have specific effects on mating. Some of these differences have already been mentioned in previous sections; they will be brought together in this section along with further relevant data. The following points will be discussed: *a*) fighting among resident males in the presence of females; *b*) tolerance of resident males toward satellite males; *c*) residence selection by satellite males and females; *d*) dependence of resident males on satellite males for mating; *e*) interference during mounting and copulation.

a. *Fighting among resident males in the presence of females*

A resident male may temporarily leave his residence to attack a neighboring resident male. He may then either return to his residence immediately after the first peck or jump, or he may continue attacking or be counterattacked in which case fighting ensues. Attacks generally occur more frequently in the presence of females than in their absence. Fighting actually occurs rather infrequently, but there is a difference between both the frequency and duration of fighting on large and small leks. On a large lek, fighting in the presence of females is seen only rarely and seldom lasts very long. On the small lek, fighting occurs much more frequently and may last for several minutes. Such long fights clearly have a frightening effect upon the females which adopt the long-neck posture and walk away from the fighting males to another area of the lek or fly off. Thus, fighting among males has a negative influence on the duration of the females' stay and thus on the occurrence of copulation. Attacks without subsequent fighting do not have such an effect on females (cf. Section III.D.2.b. and c.) Such severe fighting in the presence of

females does not seem to be concerned with the conquest of a residence—as opposed to territorial fighting which normally takes place in the absence of females (cf. Section III.B.2.a.)—but probably is the result of the comparatively unstable relationships among resident males on a small lek.

b. *Tolerance of resident males toward satellite males*

Resident males on small and large leks differ strikingly in their tolerance toward satellite males. Satellite males moving in tiptoe postures in the interresidential areas were normally never attacked by resident males on a small lek, but were severely and continuously attacked by resident males on a large lek. Consequently, comparatively few satellite males were present on the large leks, and their overall frequency of copulation on the large leks was low.

c. *Residence selection by satellite males and females*

On the large leks, most residences appeared to be almost inaccessible for satellite males due to the great intolerance of the resident males toward them. Such residences were usually singly-occupied during the visits of females to the lek. On the large lek in the Oosterwolde Polder, only a few of the total resident males were somewhat more tolerant and were taken as usual host by satellite males. Their residences were usually doubly-occupied during the presence of females on the lek. Another category of resident males may have existed on the large leks, in which males were just as tolerant as males whose residences were usually doubly-occupied, but were avoided as host by satellite males; these residences would also have been usually singly-occupied. Too few observations on large leks were made, however, to determine the existence of this last group with certainty. The females showed a pronounced preference for only a few of the almost inaccessible residences which were usually singly-occupied. All the other residences on the large lek were selected by the females far less often or not at all during the observation periods. The resident males on the few residences which were preferentially selected by the females reached the highest rate of copulation by far. Resident males on the less preferred residences and satellite males nearly never copulated.

On the small leks, in general, all residences were accessible for satellite males due to the great tolerance of the resident males. On only one of the six small leks observed was there a residence which was relatively inaccessible for satellite males. This residence which was relatively inacces-

sible for satellite males. This residence was sometimes singly-occupied and sometimes doubly-occupied. Among the tolerant resident males, some were taken as usual host, while others were generally avoided. During the females' visits, several satellite males were usually present on the lek, but the fraction of doubly- and multiply-occupied residences varied from lek to lek and from visit to visit; this variation depended mainly on the proportion of resident males to visiting satellite males, and on the tendency of the satellite males to concentrate on one particular residence. Among the accessible residences, females generally selected those which at that particular moment were multiply-occupied. On such a residence, either the resident male or a central satellite male that maintained himself during the visit of the female copulated. Resident males which acted most frequently as hosts and satellite males with a pronounced central status were among the individuals with the highest rates of copulation. The residence of the moderately intolerant resident male mentioned above was selected by females both while it was doubly- and singly-occupied; thus the chance that his residence was selected was apparently not dependent on the presence of a satellite male.

d. *Dependence of resident males on satellite males for mating*

On the large lek in the Oosterwolde Polder, mating on a residence took place almost exclusively when only the resident male was present. Occasionally a satellite male was present on a residence selected by a female, but copulation did not take place as long as the satellite male stayed. On the small lek, however, copulation on a residence took place most frequently on a doubly-occupied residence with either the resident male or the satellite male. If no satellite male was present on the residence selected by a female, copulation occurred only infrequently (except on the one residence which had a reduced accessibility for satellite males). Thus the presence of a satellite male on a residence lowered the chance of mating on the large lek, but raised the chance of mating on the small leks.

e. *Interference during mounting and copulation*

Interference from males outside a residence plays a minor role compared with interference among males present on the same residence. On large leks, where copulation takes place almost exclusively on singly-occupied residences, interference occurs rarely. On small leks females preferentially select and crouch on multiply-occupied residences as opposed to singly-occupied ones. On doubly-occupied residences, inter-

ference between resident male and satellite male occurs regularly. On a residence with more than one satellite male present, interference among resident male and satellite males occurs to such an extent that mating on such a residence takes place only rarely.

4. *Survey of behavior patterns and interpretations*

The behavior patterns shown by males when females are present on the lek are listed in Table 10. The occurrence of these patterns is approximately the same as indicated in the table for reactions in the male community, but two exceptions will be mentioned here. First, in the group of attacking acts, resident males on a small lek show grappling, feather pulling, and wing-beating toward satellite males; and second, in the oblique postures, satellite males on the small lek no longer adopt the normal oblique posture and the oblique posture with perpendicular bill toward resident males. Thus, in the presence of females, the differences in behavior shown by males on large leks and small leks are less pronounced.

These data, plus the increased frequency of fighting, attack, and the spread-tail forward, suggest that the level of aggression in resident males increases due to the presence of a female near their residence. This effect appears to be greater on small leks than on large leks.

The behavior shown by independent and satellite males toward females presumably expresses, at least partially, copulatory motivation; in addition, some of the behavior patterns are probably also motivated by aggression and escape. The fact that resident males show the up-tail forward, whereas satellite males do not, suggests that resident males express a higher degree of aggression in their behavior toward females.

5. *Relative frequency of copulation of independent males and satellite males*

In order to find the relative copulation frequency of independent males and satellite males, it is necessary to know the frequencies of males in each group and their respective copulation frequencies. It is possible to calculate the relative copulation frequency for each group of males on an individual lek. However, since satellite males and marginal males may visit more than one lek, it is more appropriate for some comparisons to calculate the relative copulation frequency for each group of males over groups of leks which have common male visitors. Both calculations have been made here.

Data will be presented for two observation areas: Schiermonnikoog, 1960, and the Oosterwolde Polder, 1962. The data for Schiermonnikoog

were obtained between May 4 and May 17; the data for the Oosterwolde Polder between May 16 and May 28. These specific data were used because I was able to recognize all (Schiermonnikoog) or almost all (Oosterwolde Polder) the individual males which visited the leks; such identification is necessary to determine the total number of males on groups of leks with common male visitors.

There is frequently a practical difficulty in determining which leks have common male visitors. The situation on Schiermonnikoog in 1960 was simple in that a constant group of males existed on the island during the observation period and copulation took place exclusively on the two leks AH and RW. Outside the two-week period in the beginning of May, 1960, and also in 1961 and 1962, some of the males also visited one or more other leks or display sites where I did not acquire sufficient data on copulation frequencies to determine the relative copulation frequency for the total area. The situation in the Oosterwolde Polder was not so clear. The large lek and the small lek lay at a distance of about 100 meters from each other; most satellite males and marginal males visited both these leks, and some resident males from the small lek also visited the large lek. Two other leks were located about 3 km further; unfortunately, I was not able to make observations at these two other leks long enough to determine whether males from the large and small leks also visited these leks and vice versa.

The data for the two areas are presented in Table 14. They show that the proportion of copulations by satellite males varies greatly from lek to lek. The large difference between percentage of copulations by satellite males on lek AH and lek RW which have almost identical proportions of resident, marginal, and satellite males is caused by one satellite male that visited lek AH exclusively and had an exceptionally high number of copulations (31% of the total). It is important to notice that on the large lek in the Oosterwolde Polder with 19 resident males, the 23 satellite males performed almost no copulations; this finding is due to the fact that resident males on large leks are highly intolerant toward satellite males, and the latter thus have almost no chance to copulate. It is further important to notice that on the small lek in the Oosterwolde Polder where satellite males outnumber resident males 2 to 1, the percentage of the copulations by satellite males is not significantly higher than on the leks of Schiermonnikoog where satellite males and resident males are present in equal numbers; it is possible that this result is due to increased interference among satellite males at multiply-occupied residences as their numbers become larger, but further observations will be necessary to

TABLE 14

FREQUENCY OF COPULATION AMONG THE VARIOUS GROUPS OF MALES ON SCHIERMONNIKOOG (*Schier*) (1960) AND IN THE OOSTERWOLDE POLDER (*O.P.*) (1962).

Area	Lek	Hours of observation	Number of males R	M	S	Total number of copulations	Copulations by S	Average copulations per hour	Total number of males	Number of S-males	Relative copulation frequency by S
Schier	AH	31.2	5	9	5	32	13(41%)	1.0	25	5(20%)	28%
	RW	33.2	5	9	4	39	7(18%)	1.2			
O. P.	Large	32.7	19	13	23	53	2(2%)	1.6	70	27(39%)	10%
	Small	8.8	8	13	17	8	2(25%)	0.9			

R = resident males; M = marginal males; S = satellite males

determine whether this is true. Thus, these data suggest that the copulation frequency by satellite males on a lek is affected (1) by the attractiveness of individual males on a lek, (2) by the size of a lek, and (3), on a small lek, by the relative frequency of satellite males.

The proportions of copulations by satellite males in each area were calculated from the proportions of copulations by satellite males on each lek in the area. Each proportion is weighted in accordance with the average copulation frequency per hour of observation. This weighted average was made on the assumption that the total number of copulations on each lek for a season is proportional to the frequency of copulation per hour of observation. For Schiermonnikoog, the results indicate that satellite males, which constitute 20% of the males in the area, performed 28% of the copulations. Using the χ^2-test, these proportions are not significantly different; it may thus be concluded that in this area the frequency of copulations by satellite males is approximately proportional to the frequency of satellite males. In the Oosterwolde Polder, satellite males, with a frequency of 39% in the area, performed only 10% of the copulations. The difference between these proportions is highly significant ($P < .001$); thus, in this area, satellite males copulate relatively less frequently than independent males.

Finally, it should be stressed that the data presented in this section were not gathered with these specific questions in mind. At least two possible sources of errors should be mentioned. (1) I have not tried systematically to record all the copulations that occurred during observations. (2) The time of observation on the two leks in one area was distributed irregularly both during a given day and during the observational period; in the Oosterwolde Polder I observed on the large lek more frequently in the early morning hours than on the small lek. There is no reason to assume, however, that my sample has had a biased influence on the ratio of

copulations by independent males and satellite males. On the other hand, the copulation frequency per hour per lek is strongly dependent on the weather and on the hour of the day. Since these factors were not controlled, they certainly introduce some error. The best way to overcome these problems is to have two observers gathering data at the two leks in an area at the same time.

6. *Interrelations among males and females on the lek*

a. *The choice and preference of the female*

In selecting a residence the female exerts her choice. Copulation takes place only after the female crouches. Thus the residence where the female crouches determines which residence will be the site of a copulation.

If crouching occurs at a singly-occupied residence, the female has in effect chosen the male with whom she will mate. At a multiply-occupied residence the situation is more complicated. In some cases a female has been observed to make an actual choice for one of the males on the residence by turning until she is in a parallel position to that male while in the crouched posture. Even when this is the case, however, the mutual interaction of the males at the residence is usually the most important factor determining which of the males will actually mate. Further, as explained above, resident males are more dependent on the cooperation of the crouching female than satellite males with respect to copulation. Thus, at a multiply-occupied residence not only the choice of the female, but also mutual behavior among the males determines the female's partner.

At all the leks observed, some of the residences are more frequently chosen by females than others, while some residences are never selected. As a result, the frequency of copulation varies greatly at the different residences and among the individual males. At the large leks, females show a pronounced preference for a few particular singly-occupied residences. At the small leks, the females' preference for particular residences is not as marked as on the large leks, and further, multiply-occupied residences are more frequently chosen than singly-occupied residences.

Observations of mine that continued throughout the whole season revealed that the general preference of females gradually shifts from one residence to another during the course of the season. Specific data on this shift of preference have been reported by SELOUS (1906) and by BANCKE and MEESENBURG (1958).

b. *The conjugal relations of both sexes*

Questions about the number of females which copulate with one individual male, and the number of males which copulate with one individual female can only be answered partially. The main difficulty in answering these questions is that it is always difficult and most times impossible to recognize individual females.

Males are clearly polygamous. It is frequently observed, for example, that when a number of females are present on the lek at the same time, they crowd around one or a few particular residences. On the large leks such residences are nearly always occupied only by the resident male who frequently copulates with several females in succession. On the small leks such residences are usually doubly-occupied, and both the resident male and the satellite male may mate with several females.

Individual males vary greatly in the number of copulations they perform. At the large leks most matings occur with a few particular resident males. For example, on the large lek in the Oosterwolde Polder during 9 days of observation in May, 1962, 53 copulations were observed. Fifty-nine percent of these copulations were performed by 3 of the 19 resident males. Eight of the 19 resident males never copulated. Only 2 of 23 satellite males copulated, once each; and one of these copulations could best be described as a "rape". At the small leks observed, copulations were more evenly distributed among the various males, and satellite males tend to participate much more. For example, on the lek AH on Schiermonnikoog during 48 days of observation in April, May and June, 1960, 128 copulations were observed. Twenty-seven percent of these copulations were performed by satellite males. All 5 resident males copulated and 3 of the 5 satellite males copulated. The male with the highest number of copulations was a satellite male that performed 23% of the copulations; most of the other copulations were performed relatively equally by 4 of the 5 resident males.

Some information about the second question—how many males mate with an individual female—can be obtained by following an individual female during a single visit to the lek. At large leks, a female normally visits only one residence and copulates only with the resident male on that residence. On a few occasions, however, females were observed to change residences, and, much more rarely, to copulate with different resident males in succession. The situation is approximately the same on small leks except that changing residences occurs more frequently. On the small leks, females have been observed to mate successively both

with a resident male and the satellite male on the same residence, and with males on different residences. In all cases, however, copulations with different males in succession do not occur very frequently.

It is impossible to decide whether females on successive visits to the lek choose the same residence(s) and copulate with the same male(s) with whom they have previously mated. On the large leks, however, the fact that so few males perform the overwhelming majority of copulations suggests that females do indeed frequently return to a male with whom they have previously mated. This idea is also supported by the data of MILDENBERGER (1953) who, by the end of the season, was able to recognize 7 females individually. He found that some of the females chose a particular male exclusively, while others were not absolutely consistent in their partner choice. A further complicating factor, however, is that females may visit more than one lek, and may, of course, copulate on any lek they visit.

In conclusion, both males and females may copulate with more than one partner, although in the case of females promiscuity is probably less pronounced. Further, individual males vary greatly in the number of copulations they perform and, thus, in the number of partners with whom they copulate. On the large leks mating is almost exclusively performed by resident males while on the small leks satellite males participate much more.

c. *Factors influencing the choice of the female*

The fact that females show marked preferences for particular males as copulating partners leads us to ask what features these preferred males have that distinguish them from the less preferred males, and which of these various features are likely to have a direct influence on the females' choice. Differences in behavior in the intersexual relations, in the host-guest relations, and in the mutual relations of resident males, as well as differences in morphological features of the nuptial plumage and differences in physical features and location of the residences will be discussed in this context. Further, attraction by other females and conditioning to a particular male or residence and their possible influence on the choice of the female will be discussed. Finally, specific suggestions will be offered as to how both inexperienced and experienced females actually make their choice.

(1) *Behavior in the intersexual relations.* On the small lek AH on Schiermonnikoog in 1960, specific observations were made to see whether males with the highest rates of copulation showed distinctive reactions

toward visiting females which could directly influence their choice. During the period of these observations, females visited and copulated, most frequently on one particular residence on which a particular highly preferred satellite male was nearly always present with the highly preferred resident male. These observations revealed that both the resident male and this particular satellite male showed some distinctive behavioral features more often than other males on the lek: they showed tail lifting and tail trembling in reaction to landing females, the resident male during wing fluttering, flutter jumping, and up-down movements, and the satellite male during wing fluttering, flutter jumping, and the tiptoe postures; moreover, the resident male showed a greater intensity in the up-down movements, and this activity was combined with bill thrusting more often than in other resident males on the lek. Both the resident male and the satellite male also showed a higher activity on the residence after it was selected by females than other twosomes in a corresponding situation: both showed a higher frequency of interrupting the squat, the resident male in order to perform behavior directed either toward males outside the residence, toward the satellite male, or toward the female, and the satellite male in order to perform behavior directed toward the female; moreover, during the spread-tail forward, this particular resident male showed a greater intensity—both duration and amplitude—of tail trembling than other resident males in corresponding situations. As described above, such behavior of a twosome greatly increases the chance of crouching and copulation on a small lek. It was further observed that a female sometimes leaves one residence and approaches another one where greater activity is occurring. Thus, there is some evidence that distinctive behavior in the intersexual relations shown by particular males of resident or satellite status influences residence selection in a female, and the chance that she will copulate there.

On the large leks, no such specific observations were carried out. A characteristic feature of the most successful resident males was that they had a much greater tendency to raise from the squat and to perform behavior with respect to the female than resident males in the corresponding situations on the small leks. However, I lack the necessary data to compare these successful resident males with other resident males on the large leks.

(2) *Behavior in the host-guest relations.* Host-guest relations between resident males and satellite males are strikingly different on large leks and on small leks as discussed in section III.D.3.

From this it can be concluded that the choice of the female is not directly influenced by the number of males which occupy a particular residence, but must depend on features of the individual males. In the case of a preference for a singly-occupied residence, the females' choice must depend on features of the resident male only. In the case of a preference for a doubly-occupied residence, the females' choice depends on the resident male or the satellite male or on resident male and satellite male together. That a resident male on a doubly-occupied residence may influence a female's choice is shown first by the fact that in the absence of satellite males, usual hosts are preferred to non-usual hosts, and second by the fact that females may stay and copulate with the resident male after a visting male has been forced away and has settled down on another residence. That a satellite male may influence a female's choice is shown by the fact that a certain satellite male may be chosen by females regardless of the residence on which he stays (an example of this was the satellite male on lek AH on Schiermonnikoog who had the highest rate of copulation of all males on the lek), and also by the fact that females sometimes do follow a satellite male which changes host. A female's choice may depend on both resident male and satellite male together in the following way. Frequently, a preferred satellite male chooses a preferred resident male as host; further, a resident male is, in general, more likely to tolerate a preferred satellite male and to drive off an unpreferred satellite male. These tendencies of satellite male and resident male usually bring the most attractive resident male and satellite male on the lek together on the same residence (at least on a small lek). Due to joint attraction of both its occupants, such a residence may have an increased attractiveness for females and, consequently, an increased chance to be selected.

(3) *Behavior in the mutual relations among resident males.* On the basis of observations of SELOUS, ANDERSEN (1951) suggests that there exists a hierarchy or dominance-order in the sense of SCHJELDERUP-EBBE (1921) among resident males on the lek, and that the resident males which fight very little have an undisputed claim on their residence and have the highest rank. He suggests that females have a preference for the males with the highest rank and that, consequently, these males reach the highest rate of copulation. TINBERGEN (1959), following ANDERSEN, also talks about a hierarchical order interwoven with the territorial system.

However, a hierarchical society in the sense of SCHJELDERUP-EBBE is essentially different from a territorial society in which individuals

are able to defend a territory from all other actual or potential territory owners in the group, and thus are dominant to all these other individuals in their own restricted area of ground (cf. BAERENDS & BAERENDS-VAN ROON 1950). Nevertheless, not all members of a territorial society may defend territories equally vigorously or effectively. The fact that differences of this sort occur among males does not mean, however, that there is a hierarchical social relation among those males.

Whether such differences in the vigor or effectiveness of the defense of territories occurs generally on Ruff leks can only be determined by a quantitative analysis of specific data on agonistic activities among the various resident males present on the lek. Such data have not been obtained in this study. Since agonistic activities among resident males take place primarily in the very early morning before females arrive, it would not seem possible that such differences among resident males have a direct influence on the females' choice. Nonetheless, one can well imagine that a correlation exists between the vigor and effectiveness of residence defense and the attraction for females. Such a correlation could be due to the same motivational factors influencing both residence defense and attraction for females.

(4) *Morphological features of the nuptial plumage.* Males with relatively high rates of copulation differ from other males on the lek with respect to the development of their nuptial plumage. On all leks observed, preferred males were characterized by an optimal development of the nuptial plumage, whereas males with underdeveloped plumage or with a frayed plumage copulated less or not at all. This was true for both resident males and satellite males. Thus it is likely that size and brilliance of the nuptial plumage directly influence a female's choice. This conclusion is also supported by the observations of SELOUS who noted that "handsome" males characterized by a full plumage were selected most frequently by the females.

Preferred males of either resident or satellite status were not characterized by a specific color or pattern of the plumage. (cf. Section III.C.), which is also in agreement with the report of SELOUS (1907: 378).

(5) *Physical features and location of the residences.* The residences on a lek differ from each other in the degree to which the grass is trampled down or by their hollowness. This is evidently caused by the differing times the owner and visiting satellite male(s) spend on each residence. The most preferred residences on a lek were always among the ones that showed these characteristics very clearly. It seems possible that such physical features of residences play some role in the residence selection by females.

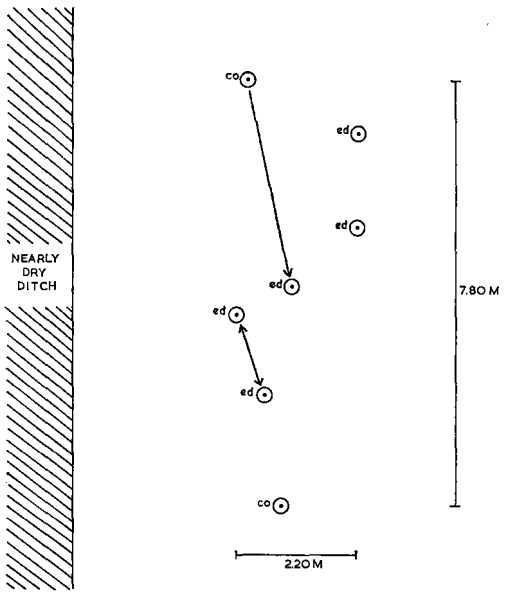


FIGURE 18. Small lek A.H. 1960, May 15, Schiermonnikoog: 5 resident males. (○ = residence; ←→ = resident male alternates between two residences; ← = resident male has replaced his residence; ed = residence in edge position; co = residence in corner position).

Residences on a lek differ in their location with respect to each other. They may be surrounded by other residences on all sides, which is called a central position. Such a location has been noted only on large leks. Residences at the edge of a large lek and most residences on small leks are not completely surrounded by other residences. Such residences with two or more neighboring residences are said to have an edge position, and those with only one neighboring residence are said to have a corner position (see Fig. 18, 19, and 20).

On the large lek in Hasselt (1961) the most preferred residence had a central position; on the large lek in the Oosterwolde Polder (1962) the two most preferred residences both had edge positions; on the small leks observed, the preferred residences had edge positions and the less preferred residences had corner positions.

Thus, it is possible that the location of a residence with respect to other residences is one of the factors influencing residence selection in females.

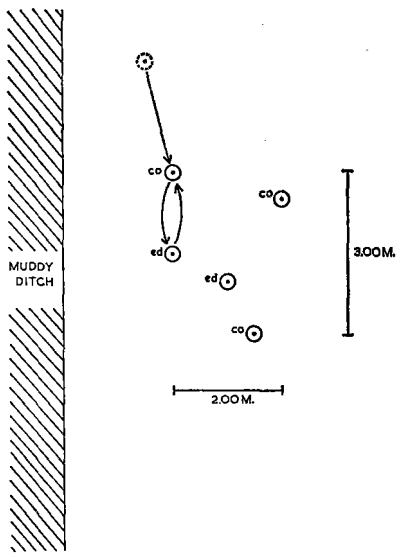


FIGURE 19. Small lek R.W. 1960, May 15, Schiermonnikoog: 5 resident males. (○ = residence; ◌ = temporary location of future resident male; → = marginal male establishes a residence — see text pp. 130, 141, 169; ←→ = two resident males exchange residences—see text p. 141; ed = residence in edge position; co = residence in corner position).

The fact that no close correlation between location and degree of preferredness exists, however, suggests that it cannot be a factor of great importance.

By conquering the residence of his neighbor, the former marginal male mentioned in section III. B. 2. a changed from a corner to an edge position on the lek; BANCKE & MEESENBURG (1958) reported several such examples. These data suggest that the choice of the female depends, at least partially, on the location of a residence.

(6) *Attraction by other females.* When several females are present on the lek at the same time, they are sometimes distributed over different residences, but usually they form one or more groups on the lek. When fighting resident males frighten them away temporarily to a remote place on the lek, they also group together. Thus it seems likely that residence selection by females is—at least to some degree—influenced by the

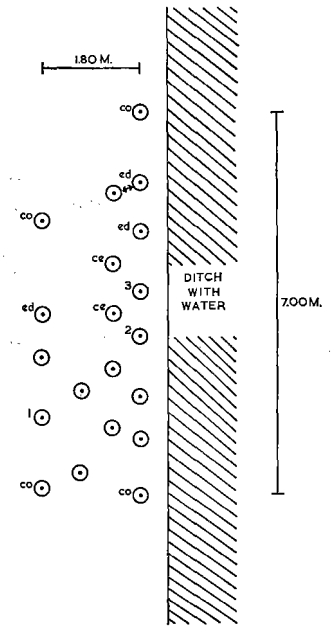


FIGURE 20. Large lek 1962, May 17, Oosterwolde Polder: 19 resident males (○ = residence; ↔ = resident male alternates between two residences; ce = residence in central position; ed = residence in edge position; co = residence in corner position; 1, 2, and 3 = resident males with highest rate of copulation (see text p. 189).

location of females already present on the lek. Further, it has been observed several times that a crouching or copulating female especially attracts other females and stimulates them to crouch also at that particular residence.

(7) *Conditioning to a particular male or residence.* It has already been concluded that a female frequently makes the same choice of residence or male on different visits to the lek. Besides the factors leading to her original choice, it is quite possible that conditioning plays a role on her later visits. It is likely that a successful copulation may act as a reinforcement for a repetition of choice. Both the location of the residence and the appearance of the copulating partner could be learned. PORTIELJE

(1931) has also pointed to conditioning processes as a possible cause of the female's choice.

The choice and preference of a female visiting a large lek seems to be different from that of a female visiting a small lek. On a large lek females almost exclusively crouch for and copulate with resident males on a few singly-occupied residences, while on a small lek females most frequently crouch for and copulate with either resident males or central satellite males on multiply-occupied residences. A possible explanation for this apparent inconsistency in behavior on the part of females will now be discussed.

The preferred residences on both large and small leks have one important feature in common: with a female nearby, the occupant(s) do not squat continuously, but interrupt squatting from time to time in order to perform other behavior. (cf. Sections III. D. 2. b and c) Crouching by a female usually takes place only after a male rises from the squat. This holds true both for the preferred males on singly-occupied residences on the large lek and for the preferred resident and central satellite males on doubly-occupied residences on the small lek. Further, males that are not preferred on the small lek—resident males on singly-occupied residences and peripheral satellites on multiply-occupied residences—generally continue squatting even when the female is near. On the large lek, similar information is not available for the singly-occupied residences since they were usually avoided by both females and satellite males; on residences that were doubly-occupied during visits of females, however, the satellite male was generally kept squatting by the ferocious attacks of the resident male, and the resident male interrupted squatting only to attack the satellite male rather than orient toward a nearby female. Thus, on both large and small leks females consistently mate with "risers" rather than "squatters".

A question still remains: how does a female distinguish between a "riser" and a "squatter". This will be discussed first for inexperienced females and then for experienced females.

Mating does not take place exclusively at preferred residences. A female is sometimes seen to visit a less preferred residence, but copulation does not usually ensue; rather, the female walks to another residence or flies off. Presumably such a female will select another residence on her next visit. By visiting different residences the female may finally, by trial-and-error, find a residence with a riser(s) which provides her with the proper stimulation to crouch. In addition, it is likely that an

inexperienced female would be influenced by some of the factors discussed above such as specific behavioral features of a male, morphological features of the male's nuptial plumage, and her attention toward other females on the lek.

An experienced female may select a partner by trial-and-error, but it is more likely that her choice depends on conditioning to a particular male or residence. Factors that influence inexperienced females may even have their effects augmented by learning. Further, an experienced female may have learned that on a small lek males on a doubly-occupied residence are more likely to interrupt squatting than a male on a singly-occupied residence; this may explain why females show a consistent preference for a twosome over a single squatting male both on the small lek and outside it (cf. Section III. D. 2. h.). The experience females have in selecting partners may explain why females sometimes crouch for a preferred resident male on a large lek before the male interrupts squatting. First, the female may recognize the male as her usual copulating partner; this presumably reduces fear in the female and increases the probability of her crouching. Second, preferred males on a large lek copulate very frequently, and it seems likely that the tendency to copulate is often higher in the female than in the male in this situation.

In conclusion, it seems clear that the choice of the female is influenced by many factors among which rising of the male from the squat and the previous experience of the female are perhaps the most important.

d. *Factors influencing the host selection of the satellite male*

On small leks where all residences were generally accessible to satellite males, the choice of both satellite males and females were clearly parallel. Among resident males with inaccessible residences, satellite males were obviously prevented from making a free choice of host. Nevertheless, the special efforts of satellite males to enter those residences preferred by females indicate that satellite males have a similar preference. Factors that influence the host selection by the satellite male will be considered here.

In the presence of females on the lek, satellite males were frequently observed to change hosts—or on large leks to try to do so—in order to enter a residence selected by a female (cf. Section III. B. 1. b.). This suggests that the females' choice may directly influence the host selection of the satellite males.

In the absence of females, however, other factors must necessarily be responsible for host selection. There are two possible ways that

could explain the parallel preferences of females and of satellite males in the absence of females. First, satellite males and females select resident males independently of each other, but both use the same characteristics in making their choice. Second, satellite males learn which residences on the lek are frequently selected by females; as with the females, either location or appearance of preferred resident males could be learned. It seems likely that both factors play a role, though the first must necessarily be of more importance at the beginning of the season when satellite males visit the lek, but females do not (though satellite males could conceivably remember a successful resident male from one season to the next).

E. Visits of the Naked-nape Males to the Lek and Their Interactions in the Lek Community

Mainly in the beginning of the season, the leks are sometimes visited by males which completely lack a nuptial plumage. They were observed singly or in groups as large as 5 at the leks in Roderwolde, a lek in Hasselt, and on Schiermonnikoog. Such males have also been noticed by Selous (e.g., 1907: 18). These naked males are most likely either young birds which will develop a nuptial plumage later in season or only in the next season, or adult birds born in a population with a more northern distribution than the Dutch population and which may develop a nuptial plumage later in the season. In the latter case, these males would be visitors stopping briefly while still on migration.

Naked-nape males are not individually recognizable like males with a nuptial plumage. They normally enter the area between the residences and walk around in an oblique posture with the bill pointing downward. Once in a while a mutual encounter occurs in which two of them orient frontally and adopt an upright posture with somewhat downward pointing bill—the oblique-bill upright and show bill thrusting or head pecking toward each other. While displaying such agonistic behavior, naked nape males are frequently charged by resident males and marginal males, whereupon they run away to another area of the lek or fly off.

On a few occasions I have observed on small leks that a naked-nape male entered a residence occupied by a resident male. The resident male reacts as if a satellite male had entered his residence: he squats. I never saw that a resident male attacked a naked-nape male on his residence. Apparently the behavior patterns shown by a naked-nape male entering a residence lack elements that release the attack in the resident male. The naked-nape does not squat, but adopts a rather horizontal posture

in which he makes turning movements toward the resident male in order to achieve a parallel position. He then tries to mount the resident male or shows intention movements of mounting. For instance, he may put one leg on the resident male's back for a moment and then take it back again; or he may hold the head feathers of the resident male in his bill while still standing next to him. He may also hold the head feathers while standing on the resident male's back, as is normal during a copulation. He does not, however, bend his legs as in a normal copulation. Once in a while a naked-nape male mounts in the reverse way, that is to say with his head oriented toward the resident male's tail. He may dismount, or he may be thrown off by the resident male. A naked-nape male may continue these activities repeatedly. The resident male reacts to a mounted naked-nape male either by remaining in the squat or by shaking him off; to a half-mounted naked-nape male, the resident male reacts either by remaining in the squat or by raising himself into the low horizontal and turning away in such a way as to hinder mounting. To naked-nape males on his residence, the resident male does not perform any of the agonistic behavior patterns of the repertoire normally directed to a satellite male on his residence. An encounter between a resident male and a naked-nape male ends when the naked-nape male finally leaves the residence.

When females are present at the lek, naked-nape males sometimes approach them by walking toward them in their usual oblique posture. The females normally walk away from them. Resident males and marginal males frequently charge naked-nape males which approach females.

I have never observed a naked-nape male that both showed mutual agonistic behavior and also entered a residence with a resident male. However, because of the low frequency of their visits to the lek and the difficulty of recognizing individual naked-nape males, it is not certain that two different groups exist. It is possible, though, that those naked-nape males showing mutual agonistic behavior will become independent males, while those entering residences will become satellite males.

IV. Descriptions of Behavior Patterns

This chapter contains descriptions of the form of the most important behavior patterns that occur on the lek in both males and females.

A. Male Behavior Patterns

Several groups of behavior patterns can be distinguished. The patterns are grouped here in the same way as in Table 10.

1. *Fighting activities*

a. *Attacking acts*

These behavior patterns are performed rather exclusively by resident males. When marginal males occasionally perform these movements, they perform them in the same way as resident males. The naked-nape males may perform pecking.

Pecking. During pecking the attacker delivers a single peck, but usually several successive pecks at the head of his opponent. The posture he assumes during pecking varies depending on the situation and on the posture of the attacked male.

During mutual fighting between independent males, pecking may occur in the ordinary forward while both opponents stand and face each other or move toward each other. Pecking may also occur while a resident male jumps against the front of his opponent's body.

During an attack on a distant male, an independent male performs pecking while in the ordinary forward. While attacking a satellite male which is squatting on his residence, a resident male performs pecking while standing in the spread-tail forward. During an attack on a satellite male standing in an oblique or upright posture on his residence, the resident male delivers the pecks while standing in the normal oblique posture.

During mutual pecking of naked-nape males, the two opponents perform pecking while standing in the oblique-bill upright.

Jumping. The attacker jumps toward the front of his opponent or jumps on his back. During mutual fighting among independent males and during an attack on a distant male, an independent male jumps from the ordinary forward. During an attack on a satellite male squatting on his residence, the resident male jumps from the spread-tail forward.

Jumping is performed by a male in order to kick or to hold on to the opponent with his feet.

Kicking. The attacker kicks his opponent simultaneously with his two feet. During mutual fighting among independent males, a male kicks by jumping with force toward the front of his opponent. In the smash, a resident male kicks his opponent while swooping down from the air on top of him. In the smash and attack, only one kick is delivered at a time; in mutual fighting several kicks in succession may be delivered.

Grappling. The attacker grapples the feathers of his opponent with his toes and bill. Grappling is usually combined with feather pull ng and wing beating. During mutual fighting among resident males,

grappling is performed after the attacker has jumped toward the front or onto the back of his opponent. When grappling is shown by a resident male toward a satellite male squatting on his residence, it is performed after the resident male has stepped or jumped onto the back of the satellite male. While standing on the back of his opponent, the attacker usually faces his opponent's head, especially when the opponent is a squatting satellite male. If the attacker manages to keep a hold on his opponent, grappling may be continued for several minutes.

Feather pulling. The attacker pulls the feathers—usually the ruff feathers—of his opponent with his bill. During mutual fighting among independent males, feather pulling is shown in combination with grappling and wing beating. Depending on whether the attacker has grappled his opponent in the front or on his back, the feathers of the front or back part of the ruff are pulled. Feather pulling by a resident male toward a satellite male squatting on his residence is performed either while standing next to the satellite male in the spread-tail forward or while grappling on the back of the satellite male. In both situations the feathers of the back part of the ruff are pulled.

Wing beating. This pattern is performed with both wings simultaneously in combination with grappling and feather pulling. Among independent males the attacker wing beats his opponent either in front or on top of his back. If wing beating is shown toward a satellite male squatting on his residence, the resident male wing beats the satellite male while standing on top of his back. If the attacker is able to keep hold on his opponent, wing beating may be continued for several minutes.

b. *Defensive acts during fighting*

Defensive acts mainly involve changes in the orientation of the head in the postures assumed during fighting. Only one completely different behavior pattern is used as a defensive act: the shake-off.

Head turning toward the side. When two opponents are facing each other and both have adopted a forward posture, one of the males may show head turning toward the side at the moment he is attacked by his opponent. In this way he may avoid the pecks delivered to his face.

Head turning toward the ground. When a male is standing on the back of his opponent with their heads facing the same direction, the mounted male usually points his head upwards trying to point his bill toward the opponent. He may, however, turn his head toward the ground and thus avoid the pecks delivered to his head.

Pulling the head back. When two opponents are facing each other,

they usually adopt a forward posture. Sometimes, however, one of the males pulls his head back with his bill still pointing at his opponent in a way that is untypical for a forward posture. In this way he avoids exposing his face to the pecks of his opponent.

Shake-off. A male mounted by his opponent may shake the opponent off his back by raising the caudal end of his body suddenly and simultaneously lowering the front part of his body. This movement is caused by a change in the posture of the legs. The shake-off may also be shown by a squatting satellite male when he is mounted by another male which attacks or tries to copulate with the satellite male.

2. *Forward postures*

The forward postures are characterized by the following features. The body axis is horizontal or pointed slightly downward; the head is lowered to the same level as the front of the body; the neck is bent in such a way that the bill points forward at first and later downward. The ruff is held as a shield in front of the body: it is fully expanded downwards, sidewards, and upwards, nearly touching the ground and brought very far forward (this is called the shield posture of the ruff). The headtufts are fully bent forward in such a way that they point forward. The legs are more or less bent. A male in a forward posture may either stand still or make trampling movements with his feet while standing or turning in place on his residence. In a forward posture, a male first faces his opponent, with his bill held in a horizontal position directed toward the opponent. Later, the bill may be directed toward the ground. At the same time, the male may turn away from his opponent until he assumes a side-tail orientation. Turning away is frequently alternated with turning toward the opponent for a while.

The forward postures may be combined with bill thrusting and tail trembling. *Bill thrusting* is a repeated thrusting movement of the head and body, first with the bill held in a horizontal position and directed toward the opponent, later with the bill directed toward the ground either while facing or turning away from the opponent. *Tail trembling* occurs with a more or less spread tail. It is a fast trembling movement of the individual tail feathers which go from side to side.

The hidden-tail forward (Fig. 3). The body axis points sharply downward; the legs are bent in such a way that the tarsi make an angle of more than 45° with the ground. The tail is closed and held in line with the body axis; the wings are folded and cover the body and tail and are folded together. The scapulars are ruffled so strongly that they stand out above the ruff.

The hidden-tail forward is frequently combined with bill thrusting, but never with tail trembling.

The ordinary forward (Fig. 4, right male and Fig. 9, left male). The body axis is usually held in a horizontal position or points slightly downward; the legs are bent in such a way that the tarsi make an angle of about 45° with the ground. The tail is held in line with the body axis or dropped slightly downwards; tail feathers may be partially spread. The wings are held slightly above the tail and are slightly separated; the wing covers are more or less raised. The ordinary forward is frequently combined with bill thrusting and sometimes with tail trembling.

The low forward. This posture is very similar to the ordinary forward; it differs in the following features: the body is held in a nearly horizontal position; the legs are bent such that the tarsi nearly touch the ground; the bill is usually turned slightly downwards; the ruff and head tufts are incompletely raised compared with other forward postures. Bill thrusting is shown with the bill pointing slightly downwards; tail trembling was not observed on the few occasions that the low forward was seen.

The spread-tail forward (Fig. 16, left male). The body is held in a slightly downward position; the legs are bent sharply such that the body is only slightly raised from the ground. The tail is usually held in a horizontal position at an angle with the body axis; it is fully spread. In assuming the spread-tail forward, the tail may be flapped up and down a few times. The wings extend above the tail and are held far apart; the wing covers are raised. In this way the tail becomes very conspicuous. The spread-tail forward is frequently combined with bill thrusting or head pecking, and tail trembling occurs nearly always.

The up-tail forward (Fig. 15, right male). The body axis points downward; the legs are bent in such a way that at first the tarsi make a wide angle with the ground; the bill is pointed forward directed toward an approaching female. The tail is bent sharply upward in a vertical position and is fully spread. The wings do not cover the body or tail, but are raised into an almost vertical position and are held far apart, in such a way that a female approaching frontally can see the tail between the two wings. Bill thrusting does not occur, but tail trembling is always combined with the up-tail forward. A male turns in this posture in such a way so as to maintain a frontal orientation with respect to a female.

3. *Oblique postures*

The oblique postures are characterized by the following features. The body axis is oblique upward at about a 45° angle with the horizontal;

the head extends above the body; the neck is more or less bent; in most oblique postures the bill points obliquely downward. The ruff and head tufts are raised in a specific way for each posture. The legs are bent as in the normal relaxed standing posture with the tarsi pointing backward slightly. In most oblique postures the tail is held in line with the body axis and covered by the wings. The oblique postures shown by resident males, marginal males, and satellite males differ in some respects, and will be described separately when necessary.

Normal oblique posture (*resident male and marginal male*) (Fig. 2, 4, 8 and 13, left male). The body axis varies rather strongly, from several degrees below to several degrees above 45°. In the former case, the normal oblique posture resembles a forward posture, but it differs in that the head is not lowered to the level of the body.

The head extends beyond the front of the body, and the neck is bent as in a normal relaxed standing posture or slightly stretched upward. The bill points obliquely downward and extends conspiously from the body and ruff. Typically, the ruff is held so that the feathers on the back of the neck form two marked ridges, while the feathers on the sides and front are less raised. The ruff has a smooth appearance on all sides. The ridges of the ruff normally extend above the head tufts which are fully bent forward.

The normal oblique posture of the resident male and marginal male may be combined with bill thrusting and with a head jerk. The *head jerk* is a sudden movement in which the head is pulled backwards and then returned to its former position immediately. During the head jerk the position of the bill and the feathers of the ruff and head tufts remains constant with respect to the head. Thus the bill remains conspicuous in independent males.

Normal oblique posture (*satellite male*) (Fig. 2 and 8, right male). The body axis does not vary so much as in the resident male; the angle with the horizontal is 45° or more. The head does not extend beyond the front of the body, but is held back. The neck is bent in a relaxed manner or is slightly stretched upward. The bill points obliquely downward and is held closely along the ruff in such a way that it does not extend beyond the ruff; the bill is thus very inconspicuous. The ruff is held in the fan posture in which the feathers in the front and back are fluffed such that they make a convex appearance from front and back, whereas the feathers at the sides of the ruff are rather relaxed. Seen from the side the ruff has the shape of a fan. The head tufts stand up from the head, but point slightly to the sides. This posture may be

combined with a head jerk. During the head jerk, the bill of the satellite male remains inconspicuous. (Fig. 8, 9 and 10, right male.)

Oblique posture with perpendicular bill (*resident male and satellite male*) (Fig. 10, left male). This posture differs from the normal oblique posture in the position of the head and bill. The head is turned down and the bill points perpendicularly toward the ground. The ruff feathers in the back of the neck point upward, and the head tufts are fully raised and bent forward in such a way that they point toward the ground; the postures of the head, bill, ruff, and head tufts are the same as in the squat.

Low-wing posture (*resident male*). The head extends less far beyond the front of the body than in the normal oblique posture. The bill points obliquely downward, and the ruff and head tufts are the same as in the normal oblique forward. The wings do not cover the body and tail, but are held somewhat loose from the body, are partially spread, and hang downward along the sides of the body with the primaries expanded halfway to the ground. This posture of the wings shows some similarity to the wing posture during copulation.

Low-wing posture with wing lifting (*resident male*). In the low-wing posture, the resident male may suddenly raise his wing and keep it raised for a few seconds. The wing is raised in a vertical plane such that the white side of the body is exposed, but the white underside of the wing is not exposed. One wing only may be raised, or both wings simultaneously.

Head-back posture (*marginal male*) (Fig. 7). The body axis lies somewhat above the 45° angle with the horizontal. The head is held far back and does not extend beyond the front of the body. The neck is bent as in the normal oblique posture of the satellite male or is stretched slightly upward. The bill is held in an inconspicuous way: it does not extend beyond the ruff and is held closely along the ruff. The ruff has a ruffled appearance and is expanded at the front side. The head tufts usually point backwards from the head. The legs, tail, and wings are held in the way that is characteristic of the oblique postures in general; the wing coverts are somewhat more raised.

The head-back posture may be combined with the head jerk. During the head jerk the ruffled appearance of the front part of the ruff is increased. The movement of the head and ruffling of the ruff together have the effect that the head and bill are hidden from a bird standing in front of him.

Strutting (*satellite male*) (Fig. 17). The body axis usually lies somewhat below the 45° angle with the horizontal. The neck is held in line with

the body axis and is slightly stretched. The head is turned downward and the bill points perpendicularly toward the ground. The ruff and head tufts are held as in the squat. The legs are bent in a special way so as to bring the body far forward; the tarsi are held in a nearly vertical position, and the ankle is bent rather sharply. The tail is held in line with the body axis or is bent slightly downward; it is fully spread and tail trembling always occurs in this posture. The wings are unfolded and are held along the sides of the body; the tips of the wings nearly touch the ground. The posture of the wings is somewhat similar to the wing posture during copulation.

4. *Upright postures*

The upright postures are characterized by the following features: The body axis points upward at an angle between 45° and 90° with the horizontal. The neck is stretched vertically upward; the legs are also stretched. The tail is held in line with the body axis; the wings are folded and cover the tail.

The upright postures shown by resident males, marginal males, and satellite males differ in some respects and will be described separately when necessary. Descriptions of hovering and the up-down movements will also be included in this section.

Sleeked upright (*independent male and satellite male*) (Fig. 6 and Fig. 13, right male). The body, neck, and legs are stretched to the extreme. The head and bill are held in a horizontal position. The ruff and head tufts are flattened, with the head tufts hanging downward along the back of the neck. In the extreme case, the feathers of ruff and head tufts are completely sleeked; in a less extreme case, the feathers of the back part of the ruff are still slightly raised and stand off slightly from the neck.

Cone upright (*resident male and marginal male*) (Fig. 5). This posture precedes or follows the sleeked upright, and differs from it in degree only. The stretching of the body, neck, and legs is less extreme. The head and bill are in a nearly horizontal position. The ruff and head tufts are not completely flattened: flattening of the feathers begins at the front and sides just below the head; the back and lower parts of the ruff are flattened later. In this way the ruff appears cone shaped, especially when viewed from the front. The head tufts point backward along the back part of the ruff.

Sleeked-front upright (*satellite male*). This posture precedes or follows the sleeked upright in the satellite male, and differs from the cone upright of the independent males in the posture of the ruff and head

tufts. The neck may be fully stretched. The feathers of the ruff are fully sleeked at the front, but are still relaxed at the sides and somewhat raised at the back part of the neck, forming two longitudinal ridges slightly standing off from the back part of the neck. The head tufts may be partially raised and spread somewhat to the side or, as the bird changes to the sleeked upright, they may lie oblique downward along the back part of the ruff. This transition in the posture of the head tufts has been chosen arbitrarily to distinguish between the sleeked-front and the sleeked upright in satellite males.

Puffed upright (*resident male*). The body axis points sharply upward. The neck is stretched into a nearly vertical position. The head and bill point sharply downward. The ruff is fully raised in front and back, but is rather relaxed at the sides, the side feathers being brought forward also. At the front the ruff has a smooth appearance, in the back it forms as in the normal oblique posture of the resident male two ridges which extend above the head and head tufts due to the position of the head. The head tufts are raised and are bent forward from the head. The wings are closed and cover the tail which is held in line with the body axis.

Circle tiptoe (*satellite male*) (Fig. 9, 11 and 12). The head and bill are held in a rather horizontal position or are turned sharply downward with the bill nearly perpendicular to the ground. The ruff is fully expanded, particularly at the sides, and is lifted up so that it encircles the head as a disk. The head tufts are raised and stand off perpendicularly from the head.

Fan tiptoe (*satellite male*). The head and bill usually point downward. The ruff usually has the fan posture as described for the normal oblique posture of the satellite male, although in the tiptoe the feathers in the front of the ruff are somewhat more lifted from the body. Thus the effect of concealing the bill is even stronger in the tiptoe than in the normal oblique posture. The head tufts stand up from the head but point slightly to the sides as in the normal oblique posture of the satellite male.

Wing fluttering (*resident male*) (Fig. 14, left male). Wing fluttering is performed in a posture that closely resembles the puffed upright. The wings are flapped up and down; in the up-stroke they are fully stretched above the body exposing the white undersides; in the downstroke they are folded and placed along the body in such a way that they do not extend sideward from the body. The tail may be more or less spread, and tail trembling may occur. The male may make trampling movements with his legs while standing or turning in one place, or he may move a few steps away from his residence.

Wing fluttering (*satellite male*) (Fig. 14, right male). The movement differs from the corresponding behavior in resident males in the position of the head, bill, ruff, and head tufts. The head and bill are held in a nearly horizontal position. The ruff has the circle posture as in the circle tiptoe, and the head tufts extend upward from the head. Due to the posture of the head, the head tufts extend above the head and ruff in contrast to the corresponding behavior pattern in the resident male.

Flutter jumping (*resident male and satellite male*). This movement is performed in the same way as wing fluttering, but instead of trampling the feet, the male makes jumps with his two legs simultaneously from the ground.

Hovering (*resident male and satellite male*). The bird beats its wings up and down so as to rise into the air directly above the residence. He may rise several meters high. The body axis is nearly horizontal; the neck and head are held in line with the body. Ruff and head tufts are held in a relaxed manner. The bill points downward. The tail is held in line with the body axis. The wings are spread sideward and are not raised as high above the body as during wing fluttering and flutter jumping; thus the white undersides are not exposed so much.

Up-down movements (*resident male*) (Fig. 15, left male). During up-down movements, the male alternately adopts an upright posture and a forward posture. The neck is somewhat stretched, and the head and bill point downward. The ruff and head tufts are raised. The ruff posture is similar to the ruff posture in a forward posture: front, sides, and back parts of the ruff are raised and brought very far forward. The tail is held in line with the body axis or points upward as in the up-tail forward. The tail may be spread and tail trembling may occur. The wings are separated and held loose from, but alongside the body.

Up-down movements may be combined with bill thrusting in such a way that the down movement of the body is shown simultaneously with the forward thrust of the bill, and the up movement of the body simultaneously with the backward movement of the head and bill.

Oblique-bill upright (*naked-nape male*). This posture closely resembles the puffed upright in form. The bill is less turned down, however, than in the puffed upright.

5. *Horizontal postures*

The horizontal postures are characterized by the following features: The body axis is horizontal. The neck is bent in such a way that the head is in line with the body axis and the head and bill point vertically

downward. The ruff and head tufts are raised; the feathers of the front of the ruff are expanded downward and brought very far forward; the feathers of the back part of the ruff are expanded upward; the back feathers at the sides of the ruff are raised and bent backward; the front feathers at the sides of the ruff are expanded sideward or somewhat forward. The head tufts are bent forward from the head and point toward the ground. The tail is held in line with the body axis.

The horizontal postures shown by resident males, marginal males, and satellite males differ in some respects and will be described separately when necessary. Also included in this section is a description of the pre-copulatory posture which has some resemblance to the horizontal postures.

Squat (*independent male and satellite male*) (Fig. 16, right male). The legs are completely folded underneath the body and the male lies with his belly and breast on the ground; the tail may be slightly off the ground. The tip of the bill touches the ground, except in a two-some, when the resident male usually places his bill on top of the head of the squatting satellite male. The wings are folded and cover the tail. While squatting, males seem to be under great tension.

Half-squat (*resident male*). The male is more or less raised from the ground; at the one extreme the tarsi make a sharp angle with the ground, while at the other extreme the tarsi are nearly perpendicular to the ground. The ruff is not expanded as fully as in the squat, and the feathers are bent further backward. The bill points vertically toward the ground; if the half-squat is continued for several minutes, the head and bill may be turned so that the bill points toward the feet. In other details, this posture closely resembles the squat.

Low horizontal posture (*resident male*). The body axis and the position of the neck, head, bill, ruff, and head tufts are the same as in the squat. The male is slightly raised from the ground due to his slightly stretched legs. The male may either stand in one place or may turn from side to side by making trampling movements with his bent legs. The tail may be spread and may show tail trembling. The wings are folded and held in a horizontal position, but may stand off from the tail somewhat, thus exposing the trembling tail feathers.

Low horizontal posture (*satellite male*). This posture closely resembles the corresponding posture of the resident male. It differs only in a quantitative manner: the satellite male usually raises himself less far from the ground than the resident male, shows tail spreading and tail trembling less often, and keeps the closed tail covered with his wings more often.

Precopulatory posture (*resident male*). The body axis points obliquely downward. The neck is bent, the head is held in line with the body axis, and the bill points obliquely downward. The ruff and head tufts are fully raised as in the horizontal postures. The legs are bent in such a way that the male is in a low position, but the tarsi make a wide angle with the horizontal. The tail is held in line with the body axis and thus points obliquely upward. The wings are folded and held in line with the body axis, but stand off slightly from the tail. The resident male normally turns in this posture with trampling movements of the legs.

B. Female Behavior Patterns

Like the male behavior patterns, some of the female behavior patterns can be grouped together. Each pattern will be described under the appropriate heading.

1. *Oblique postures*

These postures are characterized by the same general features as the male oblique postures.

Short-neck posture (Fig. 16). This posture closely resembles the normal oblique posture of independent males.

Feather touching is performed by a female in the short-neck posture, except that her head is bent down somewhat in order to reach the squatting male.

Drop-wing posture. This posture shows similarities to the low-wing posture of resident males. As with the resident male, the female may take her wings out of the supporting feathers and lower them halfway to the ground. This position of the wings shows some similarity to the wing position in the copulatory posture.

Tail-up posture. This posture differs from the drop-wing posture in that the tail is not held in line with the body axis, but points upward. This is another feature characteristic of the female copulatory posture.

2. *Upright postures*

These postures are characterized by the same general features as the male upright postures.

Long-neck posture. This posture closely resembles the sleeked upright of the males. The head and bill have a horizontal position and the feathers of head and neck are sleeked.

Oblique-bill upright. This posture is identical in form to the oblique-bill upright of the naked-nape males. The neck is stretched, and head and

bill point downward. This posture may be combined with bill thrusting and head pecking directed toward the face of other females.

3. *Other behavior patterns*

Crouching. The body axis points downward. The neck is bent, and the head is in line with the body axis or extends slightly above the body. The bill points obliquely downward. The legs are bent, but the tarsi make a wide angle with the horizontal. The tail is held in line with the body axis and points obliquely upward. The wings are folded and cover the tail. In form, this posture shows similarities with the precopulatory posture of the resident male. During crouching, the female may stand still or turn by making trampling movements with her legs.

Wingflapping. During wingflapping, the female is still in the position in which copulation took place. The body axis is horizontal, the neck is bent, and the head and bill point obliquely downward. The legs are bent with the tarsi forming a wide angle with the horizontal. The tail is in line with the body. The female then raises her wings high above her body and flaps them quickly up and down a few times without expanding them to the sides.

C. Copulation

A mounted male stands on top of the female's back and holds the female's head feathers with his bill. Both male and female are in a horizontal posture. The male then bends his legs in such a way that his tarsi lie flat on the female's back. Both male and female then spread their wings and bend them so that the wing tips touch the ground. The male then bends his tail around the female's tail and makes cloacal contact. Cloacal contact occurs for only a few seconds. The male then slides sidewards from the female's back.

V. Discussion

A. Behavioral Polymorphism in the Male Ruff

1. *Genetic control of the behavioral polymorphism*

This section is concerned with the question of whether the behaviorla differences between independent males and satellite males are genetically or environmentally controlled. Genetic control implies that the behavioral differences are due to genetic differences; environmental control implies that independent males and satellite males are identical

with respect to their morph frequencies, and the differences in their behavior are determined by environmental factors.

To settle this question definitely, breeding experiments with birds kept in confinement would have to be carried out. Such experiments have not yet been done. Therefore, at this stage, we must content ourselves with educated speculation.

In the search for factors controlling the dimorphism of independent males and satellite males, we must take into account the following findings. First, the status of independent male or satellite male is constant in successive seasons (see Section III. B. 4.). This constancy in status implies that the ontogenetic development of both independent male and satellite male is an irreversible process. Second, the observations on the behavior of naked-nape males in the lek-community (section III. E.) suggested that independent or satellite status in an individual is determined at a very early ontogenetic stage, specifically before a male develops his nuptial feathers for the first time in his life. Third, there exists an association between the behavioral differences and the morphological differences in the external appearance of the males (Section III. C). Finally, a few males of both independent and satellite status have an anomalous plumage that is characteristic of the opposite group (see Section III. C.).

In the case of environmental control, the environmental factors are necessarily of a dimorph nature to enable the dimorphism of independent males and satellite males to develop. Such environmental factors are found on the lek in the coexistence of independent males and satellite males. Thus, it is theoretically possible that the developmental direction of a young male into either an independent male or a satellite male becomes determined by his experiences on a functioning lek: his first encounters with either an independent male or a satellite male would lead to a distinctive developmental direction in the young male. This theoretical possibility, however, does not explain the association between behavior and plumage. Moreover, there would be no explanation for the evolutionary development of the behavioral dimorphism. Thus this hypothesis is extremely unlikely.

In the case of a genetical control of the behavioral dimorphism, two theoretical possibilities will be discussed: first, pleiotropy, in which one set of genes controls both behavior and plumage, and, second, linkage, in which two separate sets of genes, one controlling behavior and the other controlling plumage, are linked to a greater or lesser extent.

Pleiotropy can, theoretically, be of two kinds. First, there is direct

pleiotropy, in which the set of genes controls both behavior and plumage. In such a case it would follow that the independent or satellite status was already determined in the naked nape male. Second, there is indirect pleiotropy, in which the set of genes controls the plumage directly and the behavior indirectly. This means that the naked nape male has the potentiality of developing into either an independent male or a satellite male, but the direction of his development depends on his future plumage. Presumably the status of a male would develop in encounters with other males on a functioning lek; this could happen if the older males gave distinctive reactions to young males with a typical independent male plumage or a typical satellite male plumage. Neither case of pleiotropy, however, offers an explanation for the occurrence of males with anomalous plumage, and the second case is very unlikely because of the great variety of plumages, especially in independent males. Thus the pleiotropy hypothesis is also extremely unlikely.

Finally, there is the possibility that two separate, but linked, sets of genes control the dimorphism. This hypothesis is compatible with all four findings mentioned above (the occurrence of males with anomalous plumage can be explained by crossing over). Thus this must be regarded as the most promising hypothesis.

These considerations make it probable that we are dealing with a behavioral polymorphism that is genetically controlled. The term polymorphism is used here in the sense of FORD (1945, 1964).

2. *Balanced or transient polymorphism?*

FORD has distinguished two basic types of genetically determined polymorphism: balanced and transient. Balanced polymorphism results when "there are opposing selective forces operating which ensure that two or more allelomorphs of one gene are maintained in the population. The forces which do this usually operate in such a way that an allelomorph is at an advantage when it is rare, but at a disadvantage when it is common" (SHEPPARD 1958: 77). Transient polymorphism arises when a new advantageous form within a population is in the process of replacing the original form. Transient polymorphism is usually the result of a change in the environment, which converts a previously disadvantageous allelomorph to an advantageous one compared with the other allelomorph of the same gene.

In a balanced polymorphism it must be possible to show that the relative mating frequency of independent males and satellite males is

dependent on their respective frequencies within a population. If we assume that females generally are not distributed over more leks than males, a group of leks with common male visitors (cf. Section III. D. 5) may be considered as a population, with population defined here as a community of individuals with a communal gene pool. The necessary data could be obtained by studying a population in successive years; a less preferable method is to compare different populations. This study provides some data from different populations which have been presented in Table 14 (Section III. D. 5). From this table it can be seen that the frequencies of satellite males on Schiermonnikoog in 1960 and in the Oosterwolde Polder in 1962 are 20% and 39%, respectively. Using a χ^2-test, this difference is not statistically significant, though the data do suggest that satellite males occurred less frequently on Schiermonnikoog than in the Oosterwolde Polder. The relative frequency of copulation of satellite males in the two populations is 28% and 10%, respectively. This difference could occur by chance less than once in 100. Thus the satellite males on Schiermonnikoog copulate relatively more frequently than those in the Oosterwolde Polder. These results, considered together, tend to support the hypothesis that the relative mating frequency of independent males and satellite males are dependent on their respective frequencies within a population.

The analysis of these data given in Section III. D. 5 showed that the relative copulation frequency of satellite males on a lek—and thus in a population—was probably affected (1) by the distinct attractiveness of individual males on a lek, (2) by the size of a lek, and (3) on a small lek, by the relative frequency of satellite males. The third factor operates in such a way that the chance for successful copulation by satellite males on a small lek is greater when they are rare than when they are common. Thus there is evidence that this is one of the frequency dependent factors that are responsible for the maintenance of the two groups of males within the population. Regulation of the ratio of independent males and satellite males within a population through the second factor, lek size, will be discussed in section V.A. 3. It is difficult to conceive, however, how the first factor, individual attractiveness, could regulate the relative sizes of the two groups of males.

The relative copulation frequency is probably the most important factor in regulating the relative frequencies of independent males and satellite males within the population. It should be kept in mind, however, that other factors may be involved as well. One possibility, for example, might be that the sperms of independent males and satellite

males have a differential effectiveness: in a case where a female had copulated with both an independent male and a satellite male, such a factor could have important effects.

3. *Balancing forces*

On the basis of the data considered above, it is possible to make some speculations about the opposing selective forces that operate to ensure the behavioral polymorphism. I shall begin by distinguishing among three different types of lek: (1) large leks, on which satellite males cannot maintain themselves very long due to the intolerance of the resident males; (2) small leks with more satellite males than resident males; and (3) small leks with approximately equal numbers of satellite males and resident males. The data in Section III. D. 5 suggest that, in general, the relative copulation frequency of satellite males increases from group 1 to group 3.

Assuming that this order of relative copulation frequencies is correct, we can construct a model of how the relative frequencies of the two groups of males are regulated in the course of seasons. With respect to satellite males on small leks, an increase in their relative frequency leads to a decrease in their relative copulation frequency, while a decrease in their relative frequency leads to an increase in their relative copulation frequency. The relative frequency of independent males is regulated through the size of the lek. If it is assumed that (1) it is more attractive for an independent male to possess a residence on a large lek, and (2) the size of a large lek is limited by the average aggressiveness of resident males toward a marginal male, it follows that an individual lek will increase in size up to a certain limit, and then a new, small lek will be formed. With such a newly-formed lek the relative copulation frequency of the satellite males in the population will then increase. If the population of independent males begins to decline, the smaller lek will disappear, and satellite males will be at a disadvantage. Some evidence for the first assumption exists in the fact that 4 of the total 8 resident males from the small lek in the O.P. visited the large lek in the status of marginal male, while resident males from the large lek did not visit the small lek. The second assumption is supported by my impression during the field observations at these two leks that marginal males were frequently chased away from the large lek by the attacks, charges, and agonistic displays of the resident males, whereas resident males on the small lek showed such aggressive behavior toward marginal males much less frequently.

B. Survival Value and Evolution of the Behavioral Polymorphism

The coexistence of independent males and satellite males in the population must have survival value for the species, since the survival value of a biological phenomenon is a condition for its evolutionary development. The survival value of the existence of independent males in the population clearly lies in the fact that they establish the lek and residences, thus providing the mating places for the species. Mating outside the lek and residences normally does not take place. Thus reproduction in the Ruff is dependent on the existence of independent males in the population. The survival value of the existence of satellite males in the population is less obvious. As has been stated, on the large leks, satellite males mate only very infrequently, and resident males mate equally frequently both when satellite males are present and when they are absent. In contrast, on the small leks, the presence of satellite males does affect the copulation frequency on the lek positively. Not only do the satellite males take part in mating, but, as explained in Section III. D. 2. c, satellite males create the necessary conditions on the residences to enable resident males to attract and stimulate females to crouch for them. Thus, by their presence, satellite males increase the copulation frequency on small leks

Satellite males (and marginal males) also affect the chances for copulation in another way. When they stroll in small groups through the fields, they apparently stimulate females to join their groups and lead the females toward the leks they visit. Since satellite males are forced off large leks in an area, they will show a preference to visit small leks and will lead the females there. Thus, satellite males will promote visits of females there. Thus, satellite males will promote visits of females to the smaller leks in an area. This role of satellite males may be of importance for the establishment of a new lek. Females presumably have been conditioned to visit leks that have previously existed in their breeding area. A new lek must be discovered, and satellite males facilitate this task. In addition, this role of satellite males may be of importance in the competition for females between leks of different size and contribute to the success of leks of smaller size.

The establishment and maintenance of several leks in an area serves the purpose of enlarging the breeding area. Another advantageous effect of the existence of several leks in the same area is that more males act as copulating partners. On a large lek, most copulations are performed by only a few resident males; on the small leks, more individuals of

both resident and satellite status act as copulating partners. The biological advantage of many copulating partners is that the genetic variability is carried through to the off-spring.

Thus, the existence of satellite males in a population has survival value for the species in several ways.

Functionally, the behavioral differences between independent males and satellite males lie in the facts that:

(1) Satellite males do not establish and defend a residence of their own, but, instead, make use of the residence of a resident male while the owner is present.

(2) Satellite males show behavior patterns in which aggressive and fear motivation are predominantly absent (or, according to the alternative hypothesis, show behavior patterns in which aggressive and fear motivation are relatively well-balanced), and which have an appeasing effect on independent males.

The evolutionary development of these functions in the satellite male must have been favored by specific characteristics of the Ruff's lek-system and external appearance. Four such characteristics are suggested here.

First, there is the existence of the inter-residential areas on the lek, which are not specifically claimed by any of the resident males. On leks where resident males are relatively not very aggressive (as on small leks), these areas provide a favorable condition for other males to enter and maintain themselves, particularly for satellite males which, by means of their appeasement behavior, do not generally arouse the aggression of the resident males.

Second, there is the crowdedness of the Ruff lek, which shows that independent males have a strong tendency to remain near and to tolerate other males in their close vicinity. This provides a favorable condition for any male to approach a resident male closely, particularly a satellite male which shows appeasement behavior.

Third, there is the development of ruff and head tufts in males which favored the development of behavior patterns that differ clearly from ones shown when aggressive or fear motivation is predominant.

Fourth, there is the development of plumage diversity which favored the development of a typical (predominantly white) satellite plumage. This labeled satellite males as particular males in the community (females are also labelled distinctively by their typical appearance and size). Such a label serves the purpose of providing easy recognition of a male as a satellite male by other males.

C. Survival Value and Evolution of the Plumage Diversity in the Male Ruff

Plumage diversity among males presumably facilitates individual recognition. The individual recognition may concern either mutual recognition among males or the recognition of males by females. In discussing the survival value of these functions, it will be necessary to pay special attention to the association between behavior and external appearance among males, and to the fact that plumage diversity among independent males is much more marked than among satellite males. Mutual recognition among the various groups of males and of males by females will be discussed.

Among independent males, the tremendous diversity in plumage ensures that there are rarely resident males or marginal males that are completely similar in appearance on a single lek. Such diversity certainly facilitates mutual recognition among resident males. Mutual recognition presumably serves to reduce attack and fighting and to stabilize the interrelations among resident males on the lek. Fighting among resident males frequently results in frightening females away from the lek, and attack may lead to interference during mounting and copulation. (cf. Section III. D. 2.) Thus, both fighting and attack are disadvantageous in that they reduce the chances for successful copulation on the lek. It is possible to see how, in this way, individual recognition among resident males could have survival value for the species.

A marginal male establishing a residence on the lek gradually becomes more consistent in his choice of location on the lek. His specific appearance will easily allow nearby resident males to become accustomed to his presence, thus favoring his chances to rise to the status of resident male (cf. Section III. B. 1.). This points again to survival value of the plumage diversity among independent males.

The diversity in plumage pattern among independent males also enables both satellite males and females to recognize them individually. Satellite males could easily find back residences on which they are tolerated on large leks, and residences preferred by females on small leks. This favors the chances for copulation by satellite males. Females could find back residences on which they have successfully copulated (cf. Section III. D. 3. c.). This may have a positive influence on the copulation frequency per lek, presumably through fear reduction in the female.

There is much less plumage diversity among satellite males than among independent males, yet satellite plumage is very conspicuous and contrast strongly with the typical independent plumage. This suggests that the satellite appearance serves not so much the function of individual recognition, but more the function of satellite recognition. This function probably determines, to a large extent, the reaction of a resident male toward a male with a typical satellite plumage, thus favoring his chances to settle down on a residence. This idea is supported by the fact that satellite males with anomalous plumage (dark or colored) are generally less successful in maintaining themselves on the lek and residences. For females recognition of satellite males allows them to distinguish easily between singly- and multiply-occupied residences while approaching the lek. Further, the conspicuous white appearance of satellite males may be of importance for their function of stimulating females in the field to follow them to the lek. The fact that plumage diversity is not as extensive among satellite males as among independent males does not necessarily mean that individual recognition of satellite males, especially by females, is not important. Satellite males usually make use of a particular residence. Thus, satellite males can profit indirectly from the individually recognizable appearance of their host and the fixed location of their host's residence. This explains why plumage diversity among satellite males has not been selected for as strongly as among independent males.

Plumage diversity in such a marked way does not occur among other species of lek birds. The main difference between a Ruff lek and, for instance, leks of grouse species is the much greater crowdedness of the Ruff lek. This means that the chances for interaction and confusion among males on the Ruff lek are much greater than on the other leks, and may indicate a reason for the evidently strong selection pressure for the evolutionary development of plumage diversity. Another difference between the Ruff and other lek species concerns the absence of related species that are sympatric. Among grouse, related, sympatric species do occur, for example in North America, and are known to hybridize on leks (Prairie Chicken and Sharp-tailed Grouse, H. G. LUMSDEN, personal communication). Thus, selection against hybrids, favoring the development of species-specific features in males (cf. SIBLEY 1957) cannot have played a role in the Ruff; in other words, the development of features specific for individual males has not been counteracted by reverse selective forces. These considerations make it understandable how plumage diversity could develop in the Ruff.

VI. Summary

1. Courtship and mating in the Ruff occur on a *lek*—a communal display ground. This study, based on four seasons of field observations, investigates the social organization of the lek community and the behavior patterns that serve mutual communication among the birds; it also describes morphological features in their external appearance.

2. Very marked *sexual dimorphism* exists in both size and plumage. Males are larger than females and develop a distinctive nuptial plumage. The length and brilliance of the nuptial feathers, the size of the wattles, and the color of the legs and bill are influenced by age.

Extreme *plumage diversity* exists among males. The colors of the ruff and head tufts vary from black through brown, red, and yellow, to white. Both ruff and head tufts may be plain or show transverse striping, spots, or a pattern called the bib. The wattles show different shades of yellow and red. The values each of these dimensions assume can vary to some extent independently. Thus, completely identical males on one lek are very rare. Certain combinations of color and pattern, however, are more frequent than others. Plumage types in individual males are constant from year to year. The plumage diversity among males makes individual recognition easy.

3. A lek site consists of a number of bare spots about 30 cm in diameter and about 1 meter from each other. The bare spots are called *residences*.

Within the male community two groups can be distinguished: independent males and satellite males. The group of *independent males* can be subdivided into *resident males* and *marginal males*; the group of *satellite males* can be subdivided into *central* and *peripheral satellite males*. These distinctions are based on differences in territoriality and attachment to the lek and in the behavior patterns shown by the various groups of males. Resident males possess a residence which they occupy nearly continuously during the day, and which they defend from other independent males. After their nocturnal absence, each resident male returns to his own residence. Marginal males stay at the edge of the lek outside the residences. They visit the lek only infrequently. Occasionally severe territorial fighting is seen among resident males, which may lead to the conquest of another one's residence. The resident male which loses his residence usually leaves the lek and returns only in the status of marginal male. A marginal male may acquire resident status by establishing a residence at the edge of the lek. In contrast to resident males, many marginal males visit different leks. Satellite males do not possess a residence of their own. Rather, they make use of the residences of the resident males in the presence of the owner. A satellite male is never seen to show any form of overt aggressive behavior toward his host. The reaction of the visited resident male is highly variable: he may try to expel the satellite male by attacking him, or he may allow the satellite male to enter his residence and to remain there with him—in the latter case, the resident male shows behavior toward the satellite male that is similar to the behavior shown toward a female. The reaction of a resident male depends on the individuals involved; further, resident males on large leks are consistently less tolerant toward a visiting satellite male than resident males on small leks. One to three satellite males may visit the same residence at a time.

Although an individual satellite male usually shows a preference for one or a few particular resident males, satellite males frequently change hosts; they also visit different leks. Satellite males spend more time on small leks than on large leks because of the intolerance of resident males on the latter. Central satellite males spend relatively more time on the lek and its residences than peripheral satellite males which are easily driven off to the edge of the lek by resident males. As one extreme, a specific satellite male which visited a particular small lek almost exclusively spent nearly as much time there as the resident males.

In interactions among each other, resident males show fighting, attack, charge, and agonistic displays; this behavior serves the function of conquest and defense of residences, and is predominantly aggressive. Most of the time, however, resident males stay peacefully together on the lek, each on his own residence. In this situation a display posture is shown which reflects balanced agonistic motivation. Toward, marginal males, resident males show behavior similar to that shown among each other, but marginal males react with overt escape behavior or with displays in which escape components are very marked. Among marginal males, interactions usually do not occur, though on rare occasions behavior similar to that shown among resident males is seen. Toward satellite males, on large leks, resident males show attack, charge, and agonistic displays—behavior which is predominantly aggressive; on small leks, resident males show behavior with relatively balanced agonistic motivation. Toward resident males, on large leks, satellite males primarily show behavior in which aggressive components are predominantly absent, but a few escape components are recognizable; while, on a small lek, the central satellite males frequently show behavior in which both aggressive and escape components are predominantly absent, and which evidently has a strong appeasing effect on the resident males; the performance of such behavior patterns evidently enables the satellite males to enter and stay on a residence in the presence of the owner. The distinctive reaction of resident males toward satellite males on small and large leks must be the result of a difference in the activation of aggression in the resident males.

Transformations between independent male and satellite male occur neither within a season, nor between successive seasons. A very few males of both groups (less than 3%) occasionally show behavior in some respects characteristic of the opposite group (anomalous behavior). The status of individuals within the independent males and satellite males is influenced by age. The independent male begins in the status of marginal male, with increasing age he acquires the status of resident male, and still later in life probably loses his resident status and becomes a marginal male again. Satellite males change status from peripheral to central as they grow older. Males with anomalous plumage (see below) appear to have a reduced chance to acquire resident status (for independent males) or central status (for satellite males). Of more than 200 males observed, about 38% were satellite males.

Analysis of the plumage diversity within each group of males led to the conclusion that behavior was highly correlated with the color of the plumage: the typical plumage of independent males has black or dark-colored ruff and head tufts or a white (or almost white) ruff with black head tufts; the typical plumage of satellite males has a white or almost white ruff and head tufts or,

somewhat less common, a white or almost white ruff with colored head tufts. Anomalous plumage among independent males and satellite males was seen in 11% and 9% of the cases, respectively.

Females visit the lek for short periods. After landing they place themselves near a residence where they usually remain during their total stay at the lek. They may also move around in the interresidential area to visit other residences. They sometimes step on a residence and crouch and copulate. Only males on a residence (either resident male or satellite male) copulate. Females visit more than one lek.

Females normally approach the lek by air. The males on the lek may react with a sequence of very conspicuous displays called the reception ceremony. After the females have landed, the resident males sink into the squat and freeze in that posture on their residence; satellite males, after having selected a residence, squat and freeze together with the resident male. Females may visit either a singly-occupied residence (resident male only) or a multiply-occupied residence (resident male and one or more satellite males). A resident male and/or satellite male may interrupt squatting from time to time by raising themselves slightly and turning from side to side; the resident male is usually oriented with his tail toward the female, while the satellite male usually faces the female. A resident may also interrupt squatting to attack or to show agonistic displays toward a satellite male on his residence; this may result in expelling the satellite male. A resident male may also interrupt squatting to attack or charge males outside his residence or to show agonistic displays toward such males, while staying on his residence. A satellite male interrupts squatting only to perform behavior directed toward a nearby female. Females are evidently stimulated to step onto the residence and crouch during such interruptions of the squat. Copulation may then ensue. On a doubly-occupied residence, the satellite usually has an opportunity to copulate successfully in the short period that the resident male is absent from the residence during a charge or attack on outside males; the resident male usually copulates just after he has expelled the satellite male; when both males are present, interference frequently inhibits successful copulation. The presence of females increases the aggressive behavior shown by resident males toward satellite males; females do not have a similar effect on satellite males. Fighting among resident males also increases in the presence of females, especially on small leks. Excessive fighting has a frightening effect upon females. On large leks, resident males alone on their residences are almost exclusively the copulating partners; on small leks, the presence of satellite males on a residence increases the chances for copulation for both resident males and satellite males. In one area with two leks, the frequency of copulations by satellite males was approximately proportional to their frequency; in another area with two leks, satellite males copulated relatively less frequently than independent males. Both males and females may copulate with more than one partner, although in the case of females promiscuity is probably less pronounced. Females choose the residence on which they will copulate. Certain residences (and thus particular resident males and/or satellite males) are chosen much more frequently than others. The choice of the female appears to depend mainly on individual characteristics in the behavior and plumage of the males, especially rising from

the squat; the previous experience of the female also seems to play an important role. Similar factors are involved in the host selection of the satellite males.

Infrequently males without a nuptial plumage (*naked-nape males*) temporarily visit a lek. These birds are probably either young birds or birds from a more northern population which develop their plumage later in the season.

4. Except for the fighting activities, *behavior patterns* were grouped according to the position of the body axis. Attacking activities and forward postures are shown only by independent males. Oblique, upright, and horizontal postures are shown by both independent males and satellite males; between the two groups of males, these postures differ primarily in that independent males hold their bill in a conspicuous position, whereas satellite males tend to conceal their bill in the ruff.

5. It is argued that the Ruff provides an example of *balanced behavioral polymorphism*. A model has been constructed of how the balancing forces operate to ensure the behavioral polymorphism. It is suggested that the survival value of satellite males lies in the facts that 1) their presence increases chances for copulation on small leks and 2) they promote the establishment of new leks and the maintenance of several leks in an area. It is suggested that the marked plumage diversity among independent males serves to facilitate individual recognition by both females and other males; the less marked plumage diversity among satellite males serves primarily to identify satellite males as such to both females and other males. The evolution of both the behavioral and morphological polymorphism is briefly discussed.

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VIII. Samenvatting

1. Bij de Kemphaan worden de balts en de paring in hoofdzaak uitgevoerd op een gemeenschappelijke baltsplaats, de z.g. *lek*. Gedurende vier seizoenen werd in het veld de sociale organisatie van de lek-gemeenschap bestudeerd waarbij veel aandacht werd besteed aan de gedragspatronen door middel waarvan de vogels zich met elkaar kunnen verstaan. Ook de uitwendige morfologische kenmerken van de vogels werden in het onderzoek betrokken.

2. De grootte en het verenkleed van de vogels vertonen een zeer uitgesproken *sexueel dimorfisme*. De mannetjes zijn groter dan de wijfjes en ontwikkelen een typisch baltskleed. De lengte en de glans van de veren van dit kleed, de grootte van de wratjes om de snavel en de kleur van poten en snavel zijn afhankelijk van de leeftijd.

Tussen individuele mannetjes bestaan gewoonlijk zeer grote verschillen in de kleur van het verenkleed. De kleuren van de *kraag* en de *pluimen* op de kop kunnen van zwart via bruin, rood en geel tot wit variëren. Kraag en pluimen kunnen voorts effen zijn, maar ook dwarse strepen of stippen vertonen, terwijl soms een patroon aanwezig is dat men als „slab" zou kunnen aanduiden. De *wratjes* kunnen verschillende tinten geel en rood hebben. De kleuren en patronen der verschillende structuren kunnen betrekkelijk onafhankelijk van elkaar variëren. Op dezelfde plek treft men zelden volkomen identiek gekleurde mannetjes aan. Toch komen sommige kleurpatronen veelvuldiger voor dan andere. Individuele mannetjes vertonen van jaar tot jaar hetzelfde type verenkleed. De mannetjes zijn aan hun individuele verenkleed gemakkelijk te herkennen.

3. Een lek bestaat uit een aantal kale plekken (diameter ± 30 cm) op ongeveer 1 meter afstand van elkaar (*bonken*).

Binnen de gemeenschap van de mannetjes kan men twee groepen onderscheiden: *onafhankelijke mannetjes* en *satellietmannetjes*. Bij de onafhankelijke mannetjes kan men weer onderscheiden: de *honkmannetjes* en de *randmannetjes*; de satellietmannetjes kan men in *centrale* en *perifere satellietmannetjes* indelen. Deze onderscheidingen berusten op verschillen in de mate waarin de mannetjes een territorium verdedigen en aan een bepaalde lek gebonden zijn en tevens op verschillen in hun gedragspatronen. Honkmannetjes bezetten gedurende de dag hun honk vrijwel voortdurend en verdedigen het tegen andere onafhankelijke mannetjes. Na 's nachts afwezig te zijn geweest keren zij 's morgens weer op hun eigen honk terug. Randmannetjes blijven aan de rand van de lek buiten de honken. Zij bezoeken de lek met onderbrekingen. Soms treedt vechten tussen honkmannetjes op, dat leidt tot de verovering van het territorium van de ander. De honkman die daarbij zijn honk kwijt raakt, verlaat gewoonlijk de lek om er slechts als een randmannetje terug te keren. Een randmannetje kan tot honkmannetje worden, wanneer hij aan de rand van de lek een honk in stand weet te houden. In tegenstelling tot de honkmannetjes bezoeken de randmannetjes verschillende leks. Satellietmannetjes hebben zelf geen honk, maar maken gebruik van dat van de honkmannetjes terwijl deze aanwezig zijn. Satellietmannetjes vertonen nooit openlijk aanvalsgedrag tegenover hun gastheer. De reactie van de laatste kan sterk variëren: hij kan trachten het satellietmannetje weg te jagen door

het aan te vallen, maar hij kan het ook toestaan het honk te betreden en er met hem te blijven. In dit laatste geval vertoont de honkman tegenover de satellietman gedrag, dat lijkt op zijn gedrag tegenover een wijfje. Hoe de reactie van een honkmannetje verloopt, wordt door beide individuen bepaald; bovendien zijn honkmannetjes op grote leks veel minder tolerant tegenover satellietmannetjes dan honkmannetjes op kleine leks. Een honk kan tegelijkertijd door één tot drie satellietmannetjes worden bezocht. Hoewel een bepaald satellietmannetje gewoonlijk een voorkeur heeft voor één of enkele bepaalde honkmannetjes wisselen zij gewoonlijk vaak van gastheer en bezoeken zij ook verschillende leks. Satellietmannetjes brengen meer tijd op kleine leks door dan op grote. Centrale satellietmannetjes brengen relatief meer tijd op de lek en de honken door dan perifere satellietmannetjes, die door de honkmannetjes gemakkelijk naar de randen van de lek worden verdreven.

De honkmannetjes veroveren en verdedigen hun honken door gedrag dat overwegend van agressieve aard is: *vechten*, *aanvallen*, *jagen* en *agonistisch vertoon* (*dreigbewegingen*). Meestentijds echter staan de mannetjes rustig op de lek, ieder op zijn eigen honk. Zij laten dan een agonistisch vertoon zien, waarin de neigingen tot aanval en vlucht meer in evenwicht zijn. Honkmannetjes gedragen zich tegenover randmannetjes juist zoals zij dat tegenover elkaar zouden doen, maar randmannetjes reageren met openlijk vluchtgedrag of met een vertoon, waarin duidelijk vluchtcomponenten aanwezig zijn. Tussen randmannetjes komt gewoonlijk geen treffen voor. Op grote leks vertonen honkmannetjes tegen satellietmannetjes hetzelfde aanvalsgedrag dat zij tegen andere honkmannetjes gebruiken, maar op kleine leks laten zij gedrag zien waarin de tegenstrijdige neigingen meer in evenwicht zijn. De satellietmannetjes vertonen op grote leks tegenover de honkmannetjes gedragspatronen waarin agressieve componenten gewoonlijk ontbreken, maar waarin wel vluchtcomponenten te herkennen zijn. Op kleine leks laten de centrale satellieten gedrag zien waarin geen agressieve of vluchtcomponenten opvallen en dat op de honkmannetjes een duidelijk aanvalsremmend effect heeft. Door dit gedrag kunnen de satellietmannetjes de honken binnentreden en er samen met de honkman verblijven. Het verschil in reactie van de honkmannen tegen de satellietmannen op kleine en grote leks moet het gevolg zijn van de mate waarin de neiging tot aanval reeds bij de honkmannetjes geactiveerd is.

De status van onafhankelijke mannetjes en van satellietmannetjes blijft dezelfde, zowel binnen één seizoen als tussen opeenvolgende seizoenen. Enkele mannetjes van beide groepen (minder dan 3 %) vertonen nu en dan gedrag dat in sommige opzichten karakteristiek is voor de tegenovergestelde groep (*anomaal* gedrag). Binnen de groepen van de onafhankelijke mannetjes en van de satellietmannetjes wordt de status van het individu door de leeftijd beïnvloed. Onafhankelijke mannetjes beginnen als randmannetjes, verkrijgen op latere leeftijd de status van honkmannetjes en verliezen deze waarschijnlijk later weer om als randmannetjes hun leven te eindigen. Perifere satellietmannetjes worden op oudere leeftijd centrale satellietmannetjes. Een anomaal verenkleed vermindert de kans dat een mannetje tot honkmannetje of tot centraal satellietmannetje opklimt. Van de ruim 200 mannetjes, die werden waargenomen, waren 38 % satellietmannetjes.

De *kleur van het verenkleed* bleek verband te houden met het gedrag: on-

afhankelijke mannetjes hebben als regel een zwarte of donker-gekleurde kraag en pluimen of een witte kraag met zwarte pluimen; satellietmannetjes hebben vrijwel steeds een witte of bijna witte kraag en pluimen of minder vaak een witte kraag met gekleurde pluimen. Een anomaal verenkleed kwam bij 11 % van de onafhankelijke mannetjes en bij 9 % van de satellietmannetjes voor.

Wijfjes bezoeken de lek gedurende korte perioden. Na te zijn neergestreken stellen zij zich bij een honk op en blijven daar meestal totdat zij de lek weer verlaten. Ook bewegen zij zich wel in de ruimte tussen de honken. Soms betreden zij een honk om er te *hurken* en te *copuleren*. Slechts de mannetjes die op een honk staan (honkman of satellietman) copuleren. De wijfjes bezoeken meer dan één lek.

Gewoonlijk naderen de wijfjes de lek vanuit de lucht. De mannetjes reageren dan met een reeks opvallende gedragingen, die de *ontvangstceremonie* is genoemd. Nadat de wijfjes zijn neergestreken, gaan de mannetjes in de *omlaag* houding en verstijven in deze houding op hun honk. Satellietmannetjes, die een honk hebben gekozen, voeren hetzelfde gedrag naast de honkman uit. De wijfjes kunnen òf een enkelvoudig bezet honk bezoeken òf een meervoudig bezet honk (honkman met één of meer satellietmannen). Beide soorten mannetjes onderbreken van tijd tot tijd de omlaag, richten zich op en draaien zich heen en weer; de honkman richt gewoonlijk zijn staart naar het wijfje, terwijl de satellietman zich meestal met de kop naar het wijfje richt. Een honkman kan ook de omlaag onderbreken voor agonistisch vertoon tegenover een satellietman op zijn honk, een vertoon dat gewoonlijk eindigt in het wegjagen van de satellietman. Een honkman kan ook de omlaag onderbreken om mannetjes buiten zijn honk aan te vallen of hen te bedreigen terwijl hij op zijn eigen honk blijft. Satellietmannetjes onderbreken de omlaag alleen om tegenover een naburig wijfje het zelfde gedrag te vertonen. De gedragingen van de mannetjes blijken de wijfjes te stimuleren om het honk te betreden waar zij tijdens onderbrekingen van de omlaag hurken. Hierop kan copulatie volgen. Op een dubbel-bezet honk geeft een korte periode waarin de honkman afwezig is om een ander mannetje te bestrijden gewoonlijk gelegenheid aan een satellietmannetje om te copuleren. Het honkmannetje kan dan copuleren direct nadat hij het satellietmannetje heeft verjaagd. Als beide mannetjes aanwezig zijn belemmert hun onderlinge interactie vaak het succes van copulatiepogingen. De aanwezigheid van wijfjes verhoogt het aggressieve gedrag van honkmannetjes tegenover satellietmannetjes; het heeft echter niet een dergelijk effect op satellietmannetjes. Als wijfjes aanwezig zijn neemt — vooral op kleine leks — het vechten tussen de honkmannetjes toe. Veel vechten verschrikt de wijfjes. Op grote leks wordt vrijwel alleen gecopuleerd door honkmannetjes die alleen op hun honk aanwezig zijn; op kleine leks vergroot echter de aanwezigheid van één of meer satellietmannetjes op het honk de kansen op copulatie voor zowel het honkmannetje als de satellietmannetjes. In een gebied met twee leks bleek de talrijkheid van copulaties door satellietmannetjes ongeveer evenredig met hun aantal. In een ander gebied met twee leks copuleerden de satellietmannetjes relatief minder vaak dan de onafhankelijke mannetjes. Zowel de mannetjes als de wijfjes kunnen met meer dan één partner copuleren, hoewel in het geval van de wijfjes promiscuïteit waarschijnlijk minder sterk uitgesproken is. De wijfjes kiezen het honk waarop zij

copuleren. Sommige honken (en dus ook sommige honkmannetjes of satellietmannetjes) worden vaker gekozen dan andere. De keuze van het wijfje schijnt vooral af te hangen van individuele eigenaardigheden in het gedrag en het verenkleed van de mannetjes; het zich oprichten uit de omlaag speelt daarbij een belangrijke rol. Ervaring van de wijfjes wordt van betekenis geacht voor de keuze van de partner. Voor de keuze van de gastheer door satellietmannetjes lijken gelijksoortige factoren te gelden als voor de partnerkeuze door de wijfjes.

Van tijd tot tijd bezoeken mannetjes zonder baltskleed (*kale-kraag mannetjes*) tijdelijk een lek. Dit zijn waarschijnlijk òf jonge mannetjes òf mannetjes van een populatie uit een meer noordelijk gebied waarvan het verenkleed pas later in het seizoen volledig ontwikkeld is.

4. Behalve voor het vechtgedrag werden de gedragspatronen ook ingedeeld naar de stand van de *lichaamsas*. Aanvalshandelingen en vooruitgerichte houdingen worden alleen door onafhankelijke mannetjes getoond. Schuine, rechtopstaande en horizontale houdingen worden zowel door onafhankelijke als door satellietmannetjes vertoond; daarbij houden de satellietmannetjes gewoonlijk hun snavel verborgen, terwijl de onafhankelijke mannetjes de snavel opvallend vertonen.

5. Er wordt betoogd, dat de Kemphaan een voorbeeld is van *uitgebalanceerd polymorfisme*. Een beeld wordt opgebouwd van de werking der krachten die met elkaar in evenwicht zijn en zo het polymorfisme van het gedrag verzekeren. Verondersteld wordt dat de satellietmannetjes in de evolutie zijn blijven bestaan doordat 1) hun aanwezigheid de kans op copulatie op kleine leks vergroot en 2) zij het stichten van nieuwe leks en het in stand houden van verschillende leks in hetzelfde gebied bevorderen. Het wordt waarschijnlijk geacht, dat het opvallende verschil in verenkleed tussen de honkmannetjes het herkennen van een individu zowel door de mannetjes als door andere wijfjes vergemakkelijkt. Doordat satellietmannetjes in verenkleed minder verschillen zouden zij door de wijfjes en door andere mannetjes in hoofdzaak als vertegenwoordigers van hun groep worden herkend. De mogelijke evolutie van het polymorfisme in gedrag en in verenkleed wordt kort besproken.