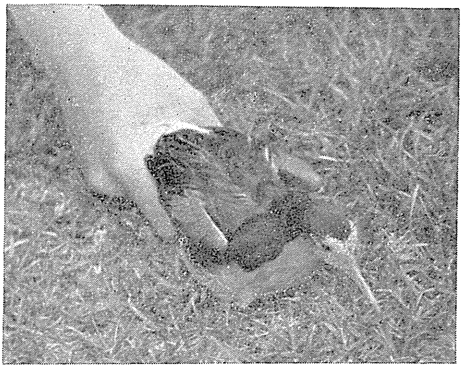

Fig. 1.

Contributions to the Biology of the Ruff (*Philomachus pugnax* (L.)) III.

By F. SØGAARD ANDERSEN.[1])

(Med et dansk resumé: Bidrag til Brushanens (*Philomachus pugnax* (L.)) biologi III.)

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Introduction.

After the second "Contribution" had been written (ANDERSEN 1948) the author had the opportunity to make observations on the sanctuary Tipperne in another season. During this season, the summer of 1948, stud. mag. P. BANCKE participated in the work, and my thanks are due to him for the splendid spirit with which he held on during the often tiring observations. I also thank him and stud. mag. E. MADSEN for handing over to me the observations made during the summer of 1949.

The present paper is the result of the observations and speculations on the ruff during this my ninth and last summer in Tipperne. It was written before I knew the book by ARMSTRONG (1947), and afterwards I discovered that my view on the behaviour of the ruff is almost identical with his, but as our approach to the problems is rather different, I still find it worth publishing.

My thanks are due to Miss A. VOLSØE for correction of the English manuscript and to Mrs. H. JØRGENSEN who read the proof.

I. Behaviour.

1) Display.

There are three questions to be answered regarding the display of the ruffs: 1) what is the function of their particular form of display? 2) how has it developed phylogenetically? and 3) which are the corresponding phenomena in other animals?

In his classic paper on the display of the ruffs SELOUS (1906 and 1907) does not pay much attention to this problem, yet he gives a kind of answer to the second question, supposing that the display developed from fighting for the reeves (1907, pp. 378—379): "That Ruffs, at one time, fought more and courted less, and that they will, as time goes on, fight still less and court still more, does not seem to me an altogether improbable supposition ..." and later: "I could almost imagine that, natural selection having first brought about the larger size, protective plumage and hard caruncalated skin of the latter (viz. the male), sexual selection had more recently got to work on all three."

CHRISTOLEIT (1924) answers the first and third questions: the ruffs have no loud voice; their common display has the same function as the song or call of other male birds, viz. to attract the females (loc. cit. p. 196). He gives a number of analogies of which that with the birds of paradise is interesting (cf. ARMSTRONG 1947, p. 239).

MAYR (1942) does not mention the ruff, but interpret the homologous display in birds of paradise (as well as all other forms of display in birds) as isolating mechanisms preventing hybridization with related species: In pair-forming birds mating is preceded by a period of engagement and a complicated display in which the female as well as the male takes part. If male and female happen to belong to different species the display goes wrong and the engagement is broken off (loc. cit. p. 255). Promiscuity in birds of paradise (and in the ruff, cf. SELOUS 1907, p. 368) excludes a long engagement, and as a deciding isolating mechanism display must therefore be very striking, allowing the female to recognize at once the males of her own species. This is accomplished by many males participating (combined with peculiar plumage).

Accepting this answer to the first and third questions, the second one (about the phylogeny) may be answered by pointing to the phylogenetic origin of isolating mechanisms as a whole (e. g. DOBZHANSKY 1941, pp. 285—287). This hypothesis is, however, based on the supposition that collective display developed as a consequence of promiscuity, but as promiscuity seems to depend on collective display, they have, no doubt, developed side by side.

In any case the first step has been that the male ceased to participate in the incubation and raising of the young. A tendency in this respect is obvious in dunlins (*Calidris*), among recent birds the closest relatives of the ruff (cf. LOWE 1915). This genus includes species in which both sexes incubate, such in which only the male incubates, as well as species in which only the female incubates (e. g. *melanotos* and *fuscicollis*).

The next step may have been a period of polygamy, which brought about the superior size of the male, as a result of the males fighting for the females (as supposed by SELOUS), but it may as well be a result of the fights of the ruffs to secure their runs (cf. p. 149).

From polygamy to promiscuity there is only a short step, since the former implies the accidental possibility of the latter, but to understand the development of the nuptial plumage and complicated display of the male, we are forced to presume influence from a closely related species (now extinct) which threatened to mix itself up with the ruff; this is a necessary condition for the development of sexual dimorphism (MAYR 1942, p. 48); the nuptial plumage and display developed then as recognition marks (loc. cit. p. 254) for the females which appear on the display ground merely when they are ready for fertilization (loc. cit. p. 260); display was now of vital importance, and the ruffs were forced to fight less (cf., however, next chapter) and court more (cf. SELOUS 1907, p. 378). The theory that in promiscuous species it is the female alone who has to decide whether she and a particular male belong to the same species or not, is perfectly borne out by the observations of SELOUS, who showed that the reeve seeks out and chooses her partner, and the modern theory of isolating thus agrees with DARWIN's theory of sexual selection.

2) **Fighting.**

In older literature it is generally held that fighting is the essential phenomenon on the display ground of the ruffs (*pugnax*!). SELOUS (1906 and 1907) was the first to show that only a minor part of the time is occupied by fighting (SELOUS 1907, p. 380): "As already intimated, I have seen no evidence of the Reeve being impressed by the fighting qualities, or by the "vigour", as such, of the male, or that these are elements of paramount importance in his courtship." and (p. 379): "His fighting, more particularly when it has directly to do with the Reeve — when her presence is the immediate cause of it — seems the outcome of a generalized state of excitement to which actual achievement bears no fixed relation. For the most it is vagrant, desultory, nor does it last long." In later literature SELOUS' view is generally accepted, e. g. by CHRISTOLEIT (1924, p. 196): "Die männlichen Kampfläufer versammeln sich nicht, um zu kämpfen, sondern um zu balzen", and MELLQUIST (1943, p. 46, translated): "Yet one has the definite impression that it is mere play and not dead earnestness".

"Dead earnest" fights may, however, be observed; SELOUS

(1907, p. 372) describes one: "These birds fought like demons, and, at the end, I noticed that the white ruff of one of them was crimsoned, here and there, about the throat" (cf. also loc. cit. pp. 175—176), and MELLQUIST (1943, p. 29) has seen blood on two ruffs. The present author has once seen a furious struggle which was continued until I was less than 10 metres from the two combatants and a long time after the other ruffs had taken off. In the following it is shown how the fighting may, nevertheless, have some bearing on sexual selection.

According to SELOUS (1907, p. 171) each ruff has a place of its own on the "hill", and only on this place pairing is accomplished; the ruff does not seek the reeves, but waits on its place for them to come. For these distinct places I suggest the name "runs" (cf. loc. cit. p. 171). The runs are clearly seen on the hills as circular places (diameter about 25 cm) where the grass is more or less worn out (cf. MELLQUIST 1943, p. 39).

Each ruff defends its run energetically, and other ruffs coming too near are driven away (MELLQUIST 1943, p. 42), and according to SELOUS (1907, pp. 172 and 173) this is the principal cause of fighting (cf. ARMSTRONG 1947, p. 219). The significance of the run is, no doubt, that here, as a rule, the ruff may copulate with a reeve without intervention from other ruffs. If interference takes place the reeve will fly away without copulation (SELOUS 1907, p. 374), and before copulation the ruff may make a rush or two against some other ruff (loc. cit., p. 176).

It is, therefore, likely that the reeves prefer to copulate with those ruffs which have a well established sovereignty over their runs, and this is, no doubt, won through fighting. However, in animals (vertebrates) living together socially the distribution of power follows the law of SCHJELDERUP-EBBE (1921) on the dominance order. This law says that among social animals a hierarchy is established, and consequently fighting occurs only when some member of the society exceptionally tries to change the order or when some animal from outside the society is involved. This law has been established in all the classes of vertebrates exept amphibians (COLLIAS 1944) and in insects (PARDI 1948), and therefore it applies, no doubt, also to the ruffs (cf. ARMSTRONG 1947, pp. 255—270).

This throws new light on many observations on the ruffs. SELOUS found that two ruffs copulated most frequently, and that the same two ruffs fought very little, whereas those who fought most, copulated very little (SELOUS 1907, p. 176). This is in accordance with what SCOTT (1948, p. 37) found (in goats), viz. that the amount of fighting is inversely proportional to the degree of dominance. In the case of ruffs it means that those with the highest degree of dominance have undisputed sovereignty over their "runs", and accordingly they copulate most frequently and need not fight.

It is, no doubt, such well established dominants, which often stay, one or two on each "hill", when the others have left (see p. 156). SELOUS (1907, p. 179) found that the brown bird and the blue one (dominates no. 1 and 2) were "almost always at home", and when only one bird was present, it was the brown one (dominant no. 1). Regarding all ruffs on a "hill" MELLQUIST (1943, pp. 38 and 40—41) distinguishes between two sentry- (uppvaktande) ruffs, which are always present on the "hill", and the others, which he calls the attendants and which, according to him, visit neighbouring "hills" (cf., however, p. 161) in bigger or smaller flocks often in compagny with some reeves, or follow the reeves on feeding trips.

That the frequency of copulation of the ruffs is "proportional" to their degree of dominance may perhaps be finally proved by simultaneous observations of the ruffs on the "hill" as well as away from it. Away from the "hill" one often watches a ruff displaying for a couple of feeding reeves and now and then rushing away to drive off some other ruff (cf. ARMSTRONG 1947, p. 223). Such observations could possibly show the hierarchy of dominance, which compared with observations on the "hill" would settle the question. In captive birds MOFFAT (1924) found that the dominant of two ruffs attracted the two reeves to himself; later, owing to beginning moult of the dominant, the former dominated male became dominant and accordingly took over the reeves (on fighting late in the season cf. p. 160).

3) Diurnal variation in activity on the "hill".

In the second "Contribution" (1948, table 10, p. 142) the diurnal variation in the activity on the "hill" is discussed on the basis of the number of ruffs caught per 100 snares per hour; the result was, however, fairly inacurate, since the number of snares per hour varied diurnally from 6 to 265, and the observations were not carried out during whole days.

In 1948 stud. mag. BANCKE and I therefore decided to spend one day a week solely for the purpose of capturing ruffs. We worked from 2 in the morning till 21 in the evening, except on 17. V., when I worked alone and had to sleep in the quiet period between 8 and 12 o'clock. A much worse drawback is that, due to our late arrival, there are no observations from the beginning of the season (cf. p. 153).

Snares were set up on the two neighbouring "hills" b and c (cf. ANDERSEN 1948, fig. 1, p. 127) at 21 o'clock the day before

Table 1.

Number of ruffs caught and snares used, 1948.
Antal Brushaner (♂♂) fanget og antal anvendte doner, 1948.

"hill" *skogger-plads*	b		c		b + c			
hour *kl.*	number of ruffs caught *antal ♂♂ fanget*	number of snares *antal doner*	number of ruffs caught *antal ♂♂ fanget*	number of snares *antal doner*	number of ruffs caught *antal ♂♂ fanget*	number of snares *antal doner*	number of ruffs caught per 100 snares *antal ♂♂ fanget pr. 100 doner*	
2—3	3	133	2	130	5	263	1.9	18.7
3—4	1	133	9	130	10	263	3.8	
4—5	3	133	5	130	8	263	3.0	
5—6	1	133	5	130	6	263	2.3	
6—7	2	133	10	128	12	261	4.6	
7—8	-	133	6	128	6	261	2.3	
8—9	1	115	1	116	2	231	0.8	
9—10	-	115	-	116	-	231	0.0	
10—11	-	115	-	116	-	231	0.0	6.9
11—12	-	115	1	116	1	231	0.4	
12—13	-	133	1	126	1	259	0.4	
13—14	-	133	-	125	-	258	0.0	
14—15	1	133	3	128	4	261	1.5	
15—16	-	133	2	131	2	264	0.8	
16—17	2	133	1	131	3	264	1.1	
17—18	-	132	2	129	2	261	0.8	
18—19	1	132	4	129	5	261	1.9	
19—20	-	132	-	129	-	261	0.0	
20—21	-	132	-	129	-	261	0.0	
total	15	2451	52	2397	67	4848		

and were inspected at 2 o'clock and at short intervals, at least once an hour. In most cases when ruffs were caught, it could be seen from the house by a telescope, and then, of course, they were immediately fetched.

The time was Central European Time which is 27 minutes ahead of local time (long. 8⁰ 13' E.).

The results concerning the diurnal variation in the activity are given in table 1 and fig. 2. The graph shows that activity starts early, the first ruffs being caught in full darkness, and a relative maximum is reached between 3 and 4 o'clock, the hour about or just before sunrise. In the following two hours the activity decreases, but between 6 and 7 there is maximum activity. This is no doubt due to the fact that by this time the sun has risen high enough to warm the ground and thus allows the incubating reeves to leave their eggs and come to the "hill". During the following two hours the activity declines, and between 9 and 14 there is a lull, only 2 out of 67 ruffs

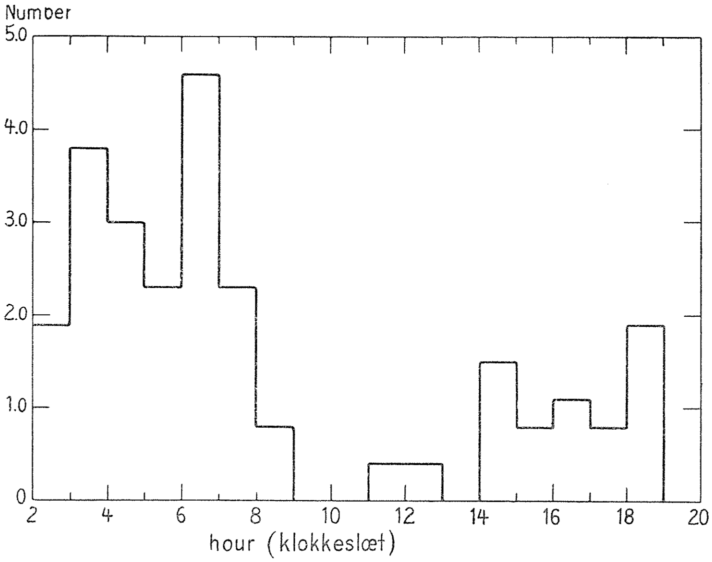

Fig. 2. Number of ruffs (♂♂) captured per hour per 100 snares; mean of 7 observations on two "hills".

Antal Brushaner (♂♂) fanget pr. 100 doner, time for time i døgnets løb; gennemsnit af 7 observationer på to skoggerpladser.

being captured during this interval. In the afternoon between 14 and 19 o'clock the maximum seems to fall between 18 and 19 (cf., however, ANDERSEN 1948, p. 142).

Finally, the table shows that the total activity between 2 and 10 o'clock is about three times as great as that between 10 and 21.

4) **Seasonal variation and influence of the weather.**

A picture of the seasonal variation in the activity on the "hill" is given in tables 2 and 3 and figs. 3 and 4. The general impression of the graphs is that the activity declines rapidly during the whole season; it is possible, however, that the season is initiated by an increase in activity: the afternoon activity (fig. 4) and the total activity on "hill" b (fig. 3) increase from the first to the second observation, and the decrease in activity on "hill" c (fig. 3) and in the morning (fig. 4) is due to the weather (cf. below); observations have unfortunately started too late to give a definite answer to this question.

Table 2.
Number of ruffs caught on the various dates in 1948.
Antal Brushaner (♂♂) fanget på forskellige datoer i 1948.

"hill" *skoggerplads*	b			c		
date *dato*	number of ruffs caught *antal ♂♂ fanget*	number of snare-hours *antal done-timer*	number of ruffs per 100 snares/hour *antal ♂♂ pr. 100 doner/time*	number of ruffs caught *antal ♂♂ fanget*	number of snare-hours *antal done-timer*	number of ruffs per 100 snares/hour *antal ♂♂ pr. 100 doner/time*
9. V.	3	262	1.1	12	227	5.3
17. V.	6	342 *)	1.8	9	209 *)	4.3
23. V.	0	304	0.0	7	353	2.0
30. V.	2	418	0.5	15	397	3.8
7. VI.	1	399	0.3	6	419	1.4
13. VI.	3	399	0.8	2	418	0.5
20. VI.	0	399	0.0	1	418	0.2
total	15	2523	0.6	52	2441	2.1

*) On 17. V. the snares were out of action from 8 to 12 o'clock; but since very few ruffs were caught at this time on the other dates, the number for comparison is calculated as if the snares had been in action continuously.

The declining activity from 9. V. to 17. V. is due to radiation fog in the morning of the latter date, the lowlying fog covering "hill" c, but not "hill" b which is about 2 m higher. The fog was observed at 3, and at 3^{05} the first two ruffs were caught on "hill" b, but no ruffs were seen on "hill" c until at 3^{50} when three males went down about at the moment when the last stars disappeared, and the "hill" used to be crowded by 15—20 birds. At 4^{17} the sun rose in a clear sky, at 4^{20} the fog had disappeared, and at 4^{30} one male was caught on each "hill". At 4^{50} the fog came back, but disappeared at 5^{00}. Until this time only one ruff had been caught on "hill" c, just as on the very unfavourable day 23. V., compared with 4 ruffs caught before five o'clock on normal days (9. V., 30. V., and

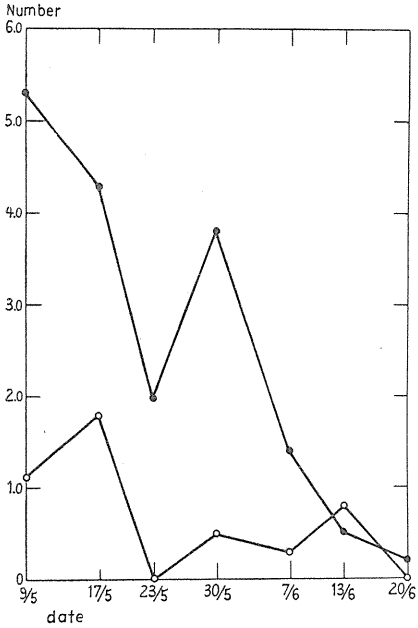

Fig. 3. Number of ruffs (♂♂) captured per 100 snares/hour on "hill" b (o—o) and on "hill" c (●—●).

Antal Brushaner (♂♂) fanget pr. 100 doner/time på skoggerplads b (o—o) *og på skoggerplads c* (●—●).

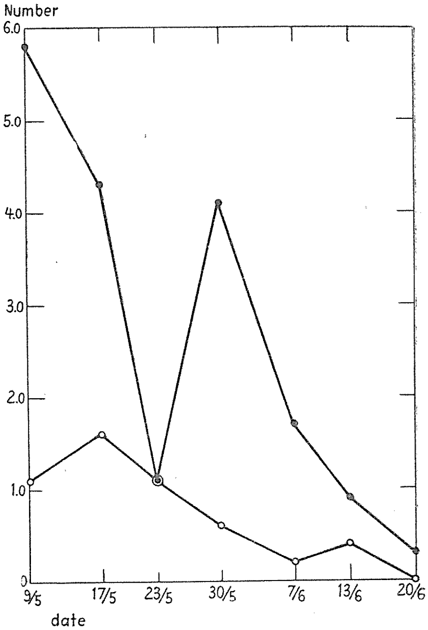

Fig. 4. Number of ruffs (♂♂) captured per 100 snares/hour on two "hills" before 10 o'clock (●—●) and after 10 o'clock (o—o).

Antal Brushaner (♂♂) fanget pr. 100 doner/time på to skoggerpladser før kl. 10 (●—●) *og efter kl. 10* (o—o).

7. VI.). On "hill" b, which rose above the fog, 3 ruffs were captured before 5 o'clock as against 2 on 9. V. and 0—1 the other days. This may be due to excitement caused by reeves seeking this "hill", the neighbouring "hill" being covered by the fog.

The steep decrease from 17. V. to 23. V. affected both "hills" (cf. fig. 3), but almost exclusively in the morning (cf. fig. 4). It was due to showers in the morning with light rain, which prevented the reeves from leaving their eggs and come to the "hill". In the afternoon it did not rain until 19^{15}, and by this time the display has generally ceased (cf. fig. 2).

Table 3.

Number of ruffs caught before and after 10 o'clock (total for the "hills" b and c).
Antal ♂♂ fanget før og efter kl. 10 (tilsammen på skoggerpladserne b og c).

	before 10 o'clock *før kl. 10*			after 10 o'clock *efter kl. 10*		
date *dato*	number of ruffs caught *antal ♂♂ fanget*	number of snare-hours *antal done-timer*	number of ruffs per 100 snares/hour *antal ♂♂ pr. 100 doner/time*	number of ruffs caught *antal ♂♂ fanget*	number of snare-hours *antal done-timer*	number of ruffs per 100 snares/hour *antal ♂♂ pr. 100 doner/time*
9. V.	12	208	5.8	3	281	1.1
17. V.	10	232 *)	4.3	5	319 *)	1.6
23. V.	3	280	1.1	4	377	1.1
30. V.	14	342	4.1	3	473	0.6
7. VI.	6	344	1.7	1	474	0.2
13. VI.	3	344	0.9	2	473	0.4
20. VI.	1	344	0.3	0	473	0.0
total	49	2094	2.3	18	2870	0.7

*) see the note to table 2.

The intensive activity in the morning on 30. V. was due to calm weather and an almost overcast sky, the clouds preventing radiation during the night and early in the morning. The reeves could therefore leave their eggs, which were not so quickly cooled as on bright mornings.

5) Individual variation in activity on the "hill".

According to the observations of Selous (1906 and 1907) and Mellquist (1943) it should be possible among all ruffs on a "hill" to distinguish a few "dominants", which are almost always there, and the other ruffs ("non-dominants"), which are present more occasionally (cf. p. 150); according to MELLQUIST the "non-dominants" visit neighbouring "hills". Do the observations on Tipperne confirm or contradict this? There are four questions to be answered:

a) Are many ruffs captured a few times each and a few ruffs caught frequently? This question is answered by table 4.

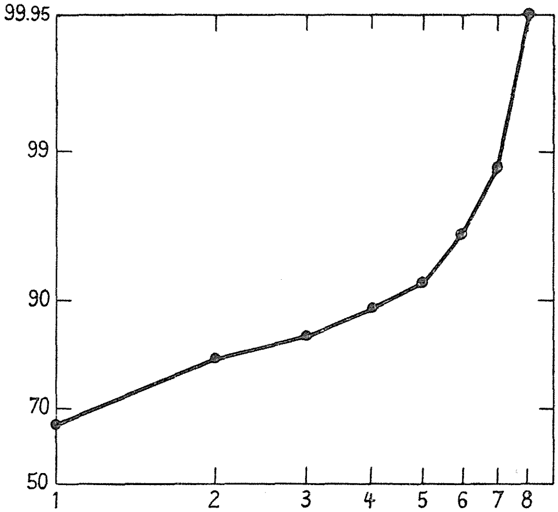

Fig. 5. Cumulative frequency distribution of ruffs according to the number of captures of each ruff. Abscissa: logarithmic; ordinate: probet. (cf. text p. 157 and table 4).

Fordeling af Brushaner efter det antal gange, de er fanget samme år (sum af resultater 1944—1948; sml. tabel 4). Abcisse: antal gange fanget (logaritmisk skala); ordinat: kumulativ frekvens-procent (probet skala). Eksempel: det tredie punkt på kurven refererer sig til alle de Brushaner, som blev fanget 3, eller færre, gange samme år ("3" på den vandrette skala); antallet af de pågældende Brushaner udgør 85 %, af det samlede antal fangne Brushaner (85 på den lodrette skala). Den lodrette skala ("probet") er således udregnet, at hvis det var tilfældigt, hvor mange gange en Brushane blev fanget, skulle kurven være en ret linie. Man ser, kurven er meget krum. Havde man ikke anvendt en logaritmisk skala til abcissen, var kurven også blevet krum. Kurven viser altså, at en uforholdsmæssig stor procentdel af samtlige Brushaner kun blev fanget 1 eller 2 gange, medens middelhyppige fangster (3—6 gange) er sjældnere, end man måtte forvente som resultat af simpel tilfældighed.

The columns marked "2" show that in all cases, but one, 53—92 $^{0}/_{0}$ (average 68 $^{0}/_{0}$) of the ruffs were captured only once, whereas the "dominants" were caught 3—8 times; the result from "hill" b 1947 points in the same direction, namely that one ruff has been much more active than all others. However, it is the logarithms of biological quantities, and generally not these quantities themselves, which are normally distributed, and the series of numbers in table 4 might therefore represent normal, logarithmic distributions. That this is not the case is clearly shown in fig. 4. In this diagram (representing the total of all observations) the logarithm of the number of times that single ruffs were caught, is plotted against the corresponding cumulative frequency-percentages on a probet scale. If the series of numbers in table 4 had represented normal, logarithmic distributions, the diagram fig. 5 would have shown a straight line, but the curve deviates from a straight line in such a way that, compared with the straight line, too few ruffs are captured a medium number of times, and too many caught only once. This first question is consequently answered in the affirmative.

Table 4.
Number of ruffs caught 1, 2, 3, ..., 8 times a season.
Antal Brushaner fanget 1, 2, 3, o. s. v. op til 8 gange i en sæson.

year ("hill") *år (skoggerplads)*	1944		1945		1946 (a + b)		1947 (b)		1947 (c)		1948 (b)		1948 (c)		total	
number of times caught *antal gange fanget*	1*	2*	1*	2*	1*	2*	1*	2*	1*	2*	1*	2*	1*	2*	1*	2*
1	3	75	6	60	9	64	0	0	11	69	11	92	9	53	49	66
2	0	75	1	70	4	93	0	0	4	94	0	92	2	65	11	81
3	1	100	1	80	0	93	0	0	0	94	0	92	1	71	3	85
4	-	-	1	90	0	93	0	0	1	100	1	100	0	71	3	89
5	-	-	0	90	1	100	0	0	-	-	-	-	1	77	2	92
6	-	-	1	100	-	-	1	100	-	-	-	-	1	82	3	96
7	-	-	-	-	-	-	-	-	-	-	-	-	2	94	2	98.7
8	-	-	-	-	-	-	-	-	-	-	-	-	1	100	1	100

1* number of ruffs (frequency). *antal Brushaner (frekvens).*
2* cumulative frequency-percentage. *kumulativ frekvens-procent.*

b) The second question is: Do the "dominant" stay on the "hill" on those times of the day, when most ruffs leave it? It appears from all observations in the years 1945—1948 that there was a general lull in the activity between 7^{30} and 13 o'clock (cf. fig. 2), and table 5 shows that the more often the ruffs have been caught (during a season), the higher was the percentage of captures in the quiet interval between 7^{30} and 13 o'clock. Thus this second question can also be answered in the affirmative.

Table 5.

Number of captures between 7^{30} and 13^{00} o'clock of ruffs caught 1—2, 3—4, 5—6, and 7—8 times a season; total 1945—1948.

Antal fangster mellem 7^{30} *og* 13^{00} *af Brushane ♂♂, som blev fanget 1—2, 3—4, 5—6 og 7—8 gange i sæsonen; sum for årene 1945—1948.*

Number of captures of the individual ruff in the season in question *Antal gange, som den enkelte Brushane blev fanget i den pågældende sæson*	1—2	3—4	5—6	7—8
A. Number of captures between 7^{30} and 13^{00} *Antal fangster mellem* 7^{30} *og* 13^{00}	6	2	6	5
B. Total number of captures *Samlede antal fangster*	68	18	28	22
A. per cent of B. *A. i procent af B.*	9	11	21	23

c) The third question is: Are the "dominants" present on the "hills" throughout the season? Table 6 throws some light on this question; it shows that the "dominants" are most active at the beginning of the season, since their part of the total number of captures is decreasing from 31 % in the first interval to 18 % (average of the three last intervals). Apart from 633116 (1946, cf. below) all "dominants" were caught in the first interval in which any ruff was captured, no "dominant" was caught in the last interval (18.—24. VI.), and two were absent in the two last intervals in which any ruffs were caught.

In table 6 the "dominant" of 1946 (633116) stands out as peculiar; it looks as if it gained its dominance after the beginning of the season and therefore remained active to the end. In this connection it may be mentioned that an old bird

Table 6.

Distribution in seven intervals of the capture of the dominant (i. e. the ruff caught most frequently on a "hill" during a season. o means no ruff caught during the interval. ÷ means ruffs captured, but not the dominant).

Fordeling på syv intervaller af fangster af dominanten (d. v. s. den Brushane, der blev fanget hyppigst på en skoggerplads i løbet af en sæson. o betyder ingen Brushaner fanget i intervallet. ÷ betyder Brushaner fanget, men ikke dominanten).

	bird no. *fugl nr.*	year *år*	"hill" *skoggerplads*	date *dato*							total
				7.—13. V.	14.—20. V.	21.—27. V.	28. V. 3. VI.	4.—10. VI.	11.—17. VI.	18.—24. VI.	
dominants *dominanter*	632048	1944	a	1	1	o	1	o	o	o	3
	632048	1945	a	o	2	1	3	o	÷	÷	6
	633116	1946	a+b	÷	1	2	÷	÷	÷	2	5
	633362	1947	b	5	o	1	o	o	o	o	6
	633610	1947	c	1	2	÷	o	o	1	÷	4
	633969	1948	b	1	÷	o	1	1	1	o	4
	633964	1948	c	3	2	1	1	1	÷	÷	8
			total	11	8	5	6	2	2	2	36
total number of captures *totale antal fangster*				36	30	20	23	11	13	9	142
dominants per cent of total *dominanter i procent af samtlige*				31	28	25	26	18	15	22	26

(632058, ringed two years before) was found dead near the "hill" (17. V.), just at the time when 633116 was captured for the first time (16. V.). Results from 1946 should, however, be handled with caution, since observations from two "hills" were not kept separate.

Thus the third question may be answered as follows: The activity of the dominants declines gradually during the season, and as a rule they are inactive in the last 1—2 weeks of the season.

Consequently, non-dominants struggling for dominance may be expected late in the season, when the dominant is inactive, and in fact SELOUS and MELLQUIST observed more fierce struggles towards the end of the season than at the beginning.

d) The fourth question is: Does the same ruff visit two neighbouring "hills"? This question may be answered by means of table 7, which shows that in 1947 and 1948 17 ruffs were captured more than once a season, and they were all recaptured on the same "hill" on which they were first captured. The total number of captures of these ruffs was 66 and the total number

Table 7.

Number of times recaptured the same year. Ruffs ♂♂.
Antal fangster og genfangster samme år. Brushane ♂♂.

year *år*	"hill" *skogger-plads*	no. *nr.*	number of times caught *antal gange fanget*	number of times recaptured *antal gange genfanget*
1947	a	632586	2	1
—	a	633352	2	1
—	b	633362	6	5
—	c	632551	2	1
—	c	633142	2	1
—	c	633143	2	1
—	c	633610	4	3
—	c	633611	2	1
1948	b	633969	4	3
—	c	633610	6	5
—	c	633684	7	6
—	c	633964	8	7
—	c	633965	5	4
—	c	633967	2	1
—	c	633968	7	6
—	c	634001	2	1
—	c	634030	3	2
		total	66	49

of recaptures was 49. However, according to MELLQUIST (1943, p. 42) only the non-dominants visit two or more neighbouring "hills", whereas the dominant stay on one "hill". It should therefore be mentioned that of the 17 ruffs listed in the table, four were dominants (cf. table 6) with a total number of 18 recaptures. Thus the total number of recaptures of non-dominants was 31, still a sufficiently large number to support the statement that as a rule ruffs did not visit more than one of the investigated "hills" during one season.

At an interval of one year a single male was, however, caught on two "hills", ruff no. 633616 being caught on "hill" c (cf. ANDERSEN 1948, fig. 1, p. 127) in 1947 (13. V. at 5^{20}) and on "hill" b in 1948 (9. V. at 4^{00}). Two other males (633610 and 633684) were caught on the same "hill" (c) in both years (1947 and 1948).

e) A fifth question may be discussed in this connection, viz. the question whether the dominants return to the same locality year after year more frequently than the non-dominants. This question may be answered by means of table 8.

Table 8.

Average number of captures of single ruffs in the year immediately preceding and following a certain year in relation to the number of times the same ruffs were caught in the year in question. 1944—1948.

Det gennemsnitlige antal fangster af de enkelte Brushaner året umiddelbart før og efter et bestemt år i forhold til det antal gange, de samme Brushaner blev fanget det pågældende år.

Number of times caught the year in question *Antal gange fanget det pågældende år*	1	2—3	4—8
Number of ruffs *Antal Brushaner*	64	22	16
Average number of times caught the preceding and the following year *Gennemsnitligt antal gange fanget året umiddelbart før og efter*	0.2	0.6	0.9

If the ruffs are arranged according to an increasing number of captures in a certain year, they show a corresponding increase in the average number of captures in the years immediately before and after the year in question. In other words the more active a certain ruff is on a "hill", the higher will be the probability of its appearance on the same locality in the preceding or following year.

Concerning the dominants data are given in table 9: one ruff was dominant in two successive years, two were caught either the year before or the year after the year of dominance, so that apart from the two dominants in 1948 (which would possibly have been captured the following year, if the investigation had been continued) one dominant only was not recorded either the preceding or the following year. (After this was written, I was informed that 633610 was captured twice and 633964 once in 1949).

Table 9.
Number of captures of the dominants.
Antal fangster af dominanterne.

no. *nr.*	"hill" *skogger-plads*	year of dominance *dominans-år*	1944	1945	1946	1947	1948
632048	a	1944 and 1945	3	6			
633116	a + b	1946			5		
633362	b	1947			1	6	
633610	c	1947				4	6
633969	b	1948					4
633964	c	1948					8

Thus the fifth question may be answered as follows: Statistically it can be stated that the more active a certain ruff is, the higher is the probability of its appearance in the preceding and the following year, but of course the individual variation is great.

6) Behaviour of the reeve.

Watching a "hill" during the breeding season, one is struck by the slow and quiet movements of the reeves compared with the violent moving about of the ruffs. This may be illustrated by the figures of capture of the two sexes by snares; 1947 gave 36 captures of ruffs and two captures of reeves, and in 1948 the figures were 67 and 4, respectively; thus males and females were captured in the ratio 17:1.

On one occasion I watched a female moving violently on a "hill": we were riding in a car and approaching a "hill" in the middle of the road just south of the sanctuary; we slowed down in order to watch the birds. As we approached most birds flew away leaving one ruff and one reeve on the "hill"; these two birds stood pointing their bills at each other, their tips about 1 cm apart, and danced round one another, faster and faster as we approached, until they looked like a fast-moving wheel just before they flew away, when the front wheel of the car was only about 1 m away.

At the nest the reeve may react towards a disturber in three different ways: 1) she may leave the nest in due time to get away unseen; 2) she may remain in the nest until one almost steps on her (unlike the redshank also on broken eggs or newly hatched young) and therefore often avoid detection; if the disturber comes too near, the reeve will rush up noisily and feign injury; or 3) she may leave the nest when the disturber is at some distance, and feign injury. Visiting many nests regularly one gets the impression that the behaviour of the reeves varies individually, some reeves behaving mainly in the first, others mainly in the second way described above; some reeves are in the nest only once out of twenty visits, whereas others are almost always in the nest.

The behaviour of the reeve changes conspicuously when the young hatch. When a disturber approaches the young, the reeve as a rule flies in circles over him uttering a low call; this way of behaviour is very seldom observed before the young hatch.

The reeve is never aggressive during incubation, but aggressiveness is not rare among reeves with young; it is no unfrequent experience to watch a reeve turning away ruffs, which are too interested in her few days old young. Once I saw a furious struggle between a blacktailed godwit (*Limosa limosa*) and a reeve, which appeared to be almost equal; walking up to the spot I found the reeve's few days old young in the godwit's nest. I even once saw a reeve take up an aggressive attitude towards a car, her ten days old young lying near the roadside; in this case the behaviour of the reeve was not unlike that of a ruff threatening.

II. Recoveries in 1948.

1) Females.

In 1948 nine reeves were caught on the nest; five of them had been ringed in the previous years. The result is shown in table 10 together with the evidence of reeves ringed in 1946 and recaptured in 1947.

The average distance was 85 m between one nest of a reeve and a nest of the same reeve one or two years later ("distance moved" in table 10), and the maximum distance was 160 m.

Table 10.

Reeves recaptured on the nest at least one year after ringing.

Brushøns ♀♀ fanget på reden mindst et år efter mærkning.

no.	date of ringing *mærknings-dato* 1946	distance moved (m) *antal m flyttet* 1946—47	date of capture *fangst-dato* 1947	distance moved (m) *antal m fllyttet* 1947—48	date of capture *fangst-dato* 1948	distance (in m) *afstand (i m)* 1946—48
730796	17. V.	60	30. V.			
730799	21. V.	130	21. V.	160	30. V.	80
730865	11. VI.	120	2. VI.			
730917			31. V.	20	28. V.	
730921			2. VI.	20	28. V.	
730813	29. V.				26. V.	115 *)
730814	29. V.	115 *)	2. VI.	30	23. V.	90 *)

*) Distance from mothers nest (730813 and 730814 were ringed as nestlings in the same nest in 1946).

Of four reeves captured on the "hills" only one (731029) was already ringed the previous year, when it was captured on the nest about 400 m from the "hill".

Thus a total of 13 reeves were captured in 1948, and of these 5 were ringed or recorded in 1947, when 26 reeves were captured out of a total population of 40. On this basis the "percentage of returnes" may be estimated at $\frac{5 \cdot 100 \cdot 40}{13 \cdot 26} = 59\,{}^0/_0$ (cf. ANDERSEN 1948, pp. 137—138). This high figure is due to the fact that the population of reeves had decreased from 40 in 1947 to 26 in 1948, and this is to a great extent due to a decrease in new-commers, since the reeve will as a rule return to the place, where it has bred.

Of the young ringed on Tipperne 2 reeves, but no ruffs, have been recaptured there; this indicates that the reeves are more likely to return to their native area; table 11 shows that otherwise the chance of recapturing ruffs would have been greater.

Table 11.
Ringing of young and capture of adult reeves and ruffs.
Mærkning af unger og fangst af voksne Brushøns af hvert køn.

	number ringed *antal mærket* 1945—1947	number captured *antal fanget* 1946—1948	number recaptured *antal genfanget* 1946—1948
♀♀	43	40	2
♂♂	47	56	0

2) **Males.**

In 1948 30 ruffs were captured on the northern "hills", and four of them had already been ringed, one in 1946 and three in 1947. In addition, one ruff was found dead in full breeding plumage about 2 km from the "hill" on which it was ringed in 1947. As in previous years the highest number of males counted simultaneously on the northern "hills" was 20; it can therefore be stated that all ruffs are seldom on the "hill" at the same time.

Calculating the "returners per cent" (cf. ANDERSEN 1948, table 5, p. 139) we get 15 % or 22 %, provided that the total number in 1947 was also 30.

It is striking that the "returners per cent" in the years 1944—1948 decreases prettily (100, 50, 42, 15) with an increasing number of ruffs captured (4, 10, 16, 18, 30). This is in accordance with the fact (cf. p. 161, table 8) that the more active a ruff is in one year, the more active is it likely to be in the following year; if, therefore, only the most active birds are caught, the calculated "returners per cent" will be too great. (In 1949 15 ruffs were captured; of these 5 were ringed previously and the "returners per cent" is calculated at 33 %).

During the six years 1944—1949 no ruff has been caught more than three years in succession.

The ratio between the numbers of ruffs and reeves is interesting. NAUMANN estimates 1:4, and CHRISTOLEIT (1924, p. 191) believes that the ratio is even more unequal. This is not the case in Tipperne; here the ruffs rather than the reeves are the more numerous, e. g. in 1948 the number of nests in the whole area was 26, compared with 30 ruffs caught on the northern "hills" only, and a number of nests in the southern part were nearer to the "hills" south of the border of the sanctuary (cf. ARMSTRONG 1947, pp. 245—246).

III. Other observations.

1) Recognition of the one-year-old birds.

It is a well-known fact that some ruffs have grey and others orange feet, and the investigation showed that this is also the case in the reeves. The fact that all young have greenish grey feet made me suppose that the colour of the feet in ruffs and reeves changes with age, and this has been confirmed by the observations of the recaptured adults.

Reeves give good evidence. Of two reeves ringed as nestlings in 1946 one was recaptured in 1947; its feet were then greenish grey. In 1948 they were both recaptured and had orange feet. In additon, orange feet have been observed in 6 cases of at least two-years-old reeves: Of the reeves captured on their nests in 1946 (when the colour of the feet was not noted) 3 were recaptured in 1947, and one of these was again captured in 1948; in all four cases they had orange feet. Of the reeves captured on their nests and ringed in 1947 three were recaptured in 1948; two of these had orange feet in both years.

The feet of the third reeve (730921) had, however, a different colour; they were in both years white or yellowish white with a reddish tinge. This may perhaps indicate high age (cf. p. 169).

In the ruffs the conditions are more complicated. Of the ruffs recaptured one year after ringing four had changed the colour of their feet: 633684 had greenish grey feet 12. VI. 1947, lead-grey 9. V. 1948, and reddish grey 17. V. 1948; 633142 had grey feet 25. V. 1946, and reddish grey 18. V. 1947; 633616 had reddish grey feet 13. V. 1947 changing to orange 9. V. 1948, and the feet of 633362 were reddish-yellowish grey 19. VI. 1946, but

23. V. 1947 the yellow tinge had almost dissappeared, the colour of the feet being almost purely reddish grey.

This seems to indicate that in the first summer as an adult the feet of the ruffs are greenish grey and in the following summer grey or reddish grey; the orange colour is not assumed until at higher age, and perhaps some individuals retain their reddish grey feet with a more or less distinct yellowish tinge (as 633362) throughout their life.

In this connection it may be of interest that of the dominants in the years 1946—1948 (cf. table 9, p. 162) not a single one had greenish grey or purely grey feet (the colour of the feet of 632048 was not recorded).

Thus it may be concluded that the feet of ruffs and reeves change colour during the first years, and after further investigations it will be a good character for recognizing at least one-year-old birds.

2) Recognition of the sex of the young.

In a previous paper (ANDERSEN 1948, p. 146) the possibility of recognizing the sex of nestlings is mentioned. We have now got more evidence for the method. Of the nestlings ringed two reeves (730813 and 730814) were recaptured, both wearing rings no. 7. In addition, the observation of two 6-days-old young (634019 and 731113) confirmed the correctness of the method; they were ringed as nestlings (June 4.) and when found (June 10.) the difference between the two sexes was obvious, the male having a larger tarsus than the female. Consequently, it is possible to recognize the sex also of young at least 6 days old, provided that both sexes are found.

3) Time of moulting of the ruff.

Throughout the mating season the feathers will dissappear gradually among the warts in the face and on the top of the head. These feathers are not replaced before the end of the mating season, and perhaps there is no clear-cut limit between this gradual disappearance of feathers from the head and the proper moulting. At any rate on 19. VI. 1946 a ruff was captured, which had lost the feathers on the top of the head also in places where there were no warts.

Moulting was more obvious in a ruff captured 20. VI. 1948; in this case new feathers were coming out on the top of the head.

In a third ruff (fig. 6) captured 21. VI. 1947 moulting was in full progress: the ear tufts and most of the ruff were lost, only a few feathers were left on the edge of the ruff, and most of the warts had disappeared. New feathers were seen on the forehead and on the neck on the ventral as well as on the dorsal side. On the sides of the breast new white feathers were coming out.

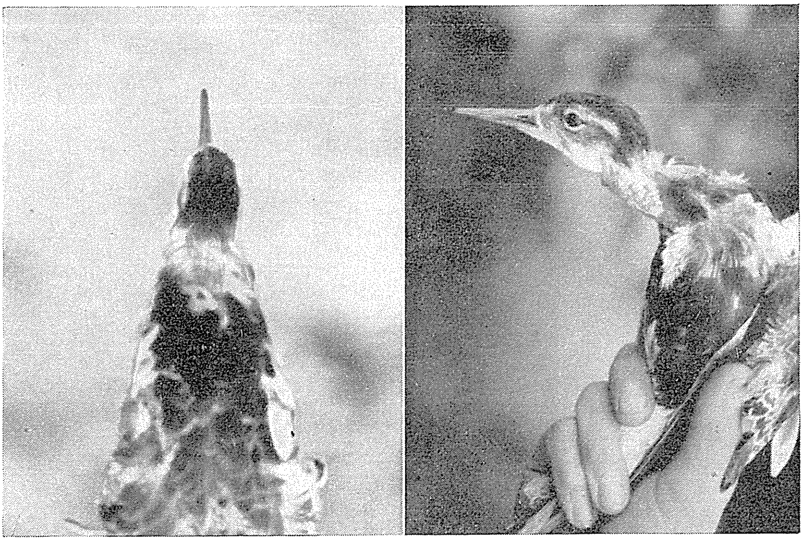

Fig. 6. Moulting in a ruff captured 21. VI. 1947.
Fældning hos en Brushane ♂ fanget 21. VI. 1947.

Thus it may be stated that in the ruffs in Tipperne proper moulting starts about June 20., or about the time when the activity on the "hills" ceases.

4) Size of eggs in relation to age of reeve.

In a previous paper (ANDERSEN 1948, p. 144) it was shown that the size of the eggs depends on qualities of the individual female. The age is one of these qualities. It is known that in fowl the size of the eggs increases during the first 2—4 years and decreases during the rest of the birds' life (ROMANOFF and ROMANOFF 1949, p. 68). Against this background, a few observations on reeves' eggs may be of interest. Table 12 gives the size of the eggs of four reeves which were captured on their nests in 1947 and 1948. Reeve no. 730814 is known to have been one year old in 1947 (cf. p. 19) and her eggs show a great increase in size from 1947 to 1948. The two reeves 730799 and 730917 were more than one year old in 1947, as they had orange feet, and their eggs show a smaller increase in size. The eggs of the reeve 730921 show a pronounced decrease in size; she was therefore probably and old bird, and as she had whitish feet, it may be possible to recognize old reeves by the colour of their feet.

Table 12.

Size of eggs of reeves captured on their nests in 1947 as well as in 1948.

no.	colour of reeve's feet	length		breadth		deviation	
		1947	1948	1947	1948	length	breadth
730814	1947 greyish green 1948 orange	43.50	44.25	30.60	31.00	+ 0.75	+ 0.40
		44.30	44.90	30.75	31.30	+ 0.60	+ 0.55
		44.35	44.90	30.80	31.30	+ 0.55	+ 0.50
		45.65	46.15	30.65	31.25	+ 0.50	+ 0.60
						+ 2.40	+ 2.05
730799	1947 and 1948 orange	44.95	44.65	31.90	32.30	— 0.30	+ 0.40
		45.05	45.05	32.40	32.80	0.00	+ 0.40
		45.20	45.70	32.65	32.20	+ 0.50	— 0.45
		45.40	45.75	32.40	32.10	+ 0.35	— 0.30
						+ 0.55	+ 0.05
730917	1947 and 1948 orange	43.85	44.10	31.95	31.90	+ 0.25	— 0.05
		44.30	44.75	32.15	32.20	+ 0.45	+ 0.05
		44.60	45.30	32.65	32.25	+ 0.70	— 0.40
		45.70	45.90	32.15	32.45	+ 0.20	+ 0.30
						+ 1.60	— 0.10
730921	1947 white with a reddish tinge 1948 yellowish white with a reddish tinge		42.80		30.75	—	—
		43.80	43.30	30.45	31.00	— 0.50	+ 0.55
		43.90	44.00	31.05	30.35	+ 0.10	— 0.70
		44.80	44.15	31.40	30.95	— 0.65	— 0.45
						— 1.05	— 0.60

5) **Rings recorded from outside Tipperne.**

Of the ruffs and reeves ringed on Tipperne five have been recorded from abroad. These records are given below.

The most interesting of these records is 632075, a male bred in Tipperne and obviously breeding in the northern U.S.S.R. Such results were to be expected, because the ruff has a wide breeding area without formation of races, and this state of affairs can be maintained only as a result of effective mixing up of the population. Perhaps this mixing is maintained in the way that the reeves return to the territory, where they were bred, but the ruffs do not; it was shown (p. 165) that the reeves are more likely to return to their native ground, and the bird recorded from Archangelsk was a male. (The possibility can not be excluded that the presence of this ruff at Archangelsk may be due to failure of homing, which is not uncommon in the ruff; thus the species is met with in Greenland, and dr. TÅNING has told me that they got one onboard the M/S Dana north of the Faeroes in August 1950).

no.	ringed	recorded
730360	16. VI. 1940 one day old	Stadthagen, W. of Hannover (about 52° 25' N. 9° 07' E.); captured, unable to fly, 26. IV. 1944. This record was already given by TÅNING (1944, p. 216), who supposes that the bird was a female.
632075	1. VI. 1944 one day old	Neighbourhood of Archangelsk (about 64° 33' N. 40° 47' E.) in spring 1946. This bird was a male; if it had been a female, it would have lost the ring. (cf. ANDERSEN 1948, p. 146).
633190	10. VI. 1946 adult male	Shot near Milano (about 45° 28' N. 9° 15' E.) 23. III. 1949.
634236	7. VI. 1949 adult male	Villers sur Mer (Calvados) (40° 19' N. 0° 00') 9. III. 1950.
634238	11. VI. 1949 adult male	Shot at Nettuno (Roma) (about 40° 56' N. 12° 37' E.) 25. II. 1950.

The two records (633190 and 634238) confirm the well known north-ward migration through Italy, while records from the Atlantic coast (634236) were not published before. These three birds are known to have belonged to the breeding stock of Tipperne since they were ringed as adults.

DANSK RESUMÉ

Bidrag til Brushanens (*Philomachus pugnax* (L.)) biologi III.

Denne artikel er resultatet af iagttagelser og spekulationer over Brushøns i ynglesæsonen 1948, forfatterens niende og sidste sommer på Tipperne.

Under en gennemgang af Brushønsenes opførsel forklares legen på skoggerpladsen analogt med MAYRS opfattelse (1942) af paradisfuglenes leg: Parringen foregår i flæng, og hunnen kommer først til skoggerpladsen, når den er rede til parring. Hvis der ikke skal ske artskrydsninger, er det derfor nødvendigt, at hunnen straks kan kende sine artsfæller. Derfor det særlige sceneri, som altså spiller samme rolle som kurmageriet i den "forlovelsestid", som går forud for parringen hos parfugle (konf. ARMSTRONG 1947). Under nogle phyllogenetiske overvejelser erindres om, at Brushanen har sine nærmeste nulevende slægtninge blandt rylerne (*Calidris*) (LOWE 1915), og at der indenfor denne slægt findes arter, hvor hannen ikke tager sig af æg og unger.

Egentlige kampe forekommer, omend sjældent, på skoggerpladsen. De forklares som territorial-kampe, hvorved hver Brushane forsøger at forsvare sin plads på skoggerpladsen. Når de er så sjældne, skyldes det, at Brushanerne etablerer en hakkeorden som den, SCHELDERUP-EBBE (1921) beskrev hos tamhønen, og kun når ordenen brydes, bliver kampene alvorlige (konf. ARMSTRONG 1947). SELOUS (1906 og 1907) fandt, at de Brushaner, der parrede sig mest, kæmpede mindst; dette stemmer med, at de individer, der står øverst i hakkeordenen sjældent behøver at forsvare deres plads.

På grundlag af systematisk fangst med doner på 7 datoer med en uges mellemrum på to skoggerpladser beskrives variationen i aktiviteten udtrykt talmæssigt som antallet af Brushaner fanget pr. 100 doner pr. time. Døgnvariationen er fremstillet i tabel 1 og fig. 2. Man ser, at den største aktivitet er om morgenen med to højdepnukter, kl. 3—4 og 6—7. Midt på dagen er der stille, og aktiviteten er svag om eftermiddagen. Sæsonvariationen beskrives i to tabeller og to diagrammer; tabel 2 og fig. 3 giver en sammenligning mellem aktiviteten på to skoggerpladser, og tabel 3 og fig. 4 viser aktiviteten før og efter kl. 10. Bortset fra uregelmæssigheder, der skyldes vejret, falder aktiviteten jævnt i løbet af sæsonen.

En undersøgelse af aktivitetens individuelle variation viser

a) at få Brushaner fanges tiere og et større antal fanges sjældnere, end man må forvente som resultat af simpel tilfældighed (tabel 4 og fig. 5),

b) at de Brushaner, som fanges flest gange, fanges oftere, end man kunne forvente, i den stille tid mellem kl. 7^{30} og 13^{00} (tabel 5),

c) at i løbet af sæsonen aftager dominanternes aktivitet hurtigere end den samlede aktivitet (tabel 6),

d) at den samme Brushane i samme sæson ikke blev fanget på mere end een af de undersøgte skoggerpladser (tabel 7), og

e) at jo mere aktiv en Brushane er på en skoggerplads et bestemt år, des større sandsynlighed er der for, at den har været der året før og/eller viser sig året efter (tabel 8 og 9).

I modsætning til Brushanen udfører Brushønen sjældent voldsomme bevægelser på skoggerpladsen; det illustreres ved, at der kun fanges en høne for hver 17 haner i donerne.

Aggressiv opførsel hos Brushønen iagttages først, når ungerne er udruget.

På grundlag af mærkninger af Brushøner fanget på reden kunne det vises, at fuglene fra det ene år til det andet flytter deres rede gennemsnitlig 85 m (tabel 10).

Af unger mærket på Tipperne er to hunner blevet genfanget, men ingen hanner. Da der af hannerne er mærket flere unger og fanget flere voksne, kan man derfor slutte, at hunnerne er mere tilbøjelige til at vende tilbage til det sted, hvor de er udruget (tabel 11).

Genfangst-procenten af hanner mærket som voksne for årene 1944—1948 aftager tydeligt (100, 50, 42, 15) med stigende antal fangster (4, 10, 16, 18, 30); det skyldes, at de mest aktive er mest tilbøjelige til at vende tilbage, og de udgør naturligvis den største procent, når man kun fanger få.

Iagttagelser ved mærkning og genfangst af Brushøns viser, at et-årige hunner kan kendes på, at de har grøngrå fødder; ældre hunner har orangefarvede fødder, og hvidlige fødder er måske tegn på høj alder. Hos hannerne er fødderne ligeledes grøngrå hos et-årige. Hos (formodede) to-årige kan farven skifte fra blygrå til rødgrå i ynglesæsonen. Den orange farve opnås sandsynligvis først, når hannen er henimod 3 år gammel.

Den tidligere fremsatte formodning (Andersen 1948, p. 146), at ungernes køn kan bestemmes ved den ringstørrelse, der passer dem, er bekræftet ved ny iagttagelser.

Fældningen af krave og øretoppe var påbegyndt hos en Brushane fanget 19. VI., og den var i fuld sving hos en fanget 21. VI. (fig. 6).

Fire hunner blev fanget på reden to år i træk; variationen i størrelsen af deres æg fremgår af tabel 12: en ung fugl viser stærkt stigende ægmål, og to ældre fugle viser svagere stigning; den sidste viser faldende ægmål, og det er sandsynligvis en gammel fugl; den havde hvidlige fødder.

Fire ny genmeldinger publiceres (p. 170).

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