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BEHAVIOURAL DIMORPHISM IN MALE RUFFS, *PHILOMACHUS PUGNAX* (L.)

by

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(With 15 Figures)
(Rec. 15-VI-1973)

CONTENTS

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1) I wish to express my gratitude to many stock-farmers, who gave me the opportunity to study Ruffs in their meadows. I particularly owe a great debt to the brothers DE BOER. They offered me a piece of their land for a temporary field lab and prevented the intrusion of cows on the arena. I also wish to thank Staatsbosbeheer for their kind permission to observe in their sanctuaries.

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I am grateful to Dr J. P. KRUIJT for his valuable advice and his critical discussion of the manuscript. I also wish to express my thanks to the other members of the research group on arena behaviour, particularly Drs I. BOSSEMA and Drs G. J. DE VOS.

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I. INTRODUCTION

Courtship and mating of the Ruff, *Philomachus pugnax* (L.), take place mainly on communal display grounds or arenas. In this arena community Hogan-Warburg (1966) distinguished two groups of males: independent males and satellite males. Her classification was based upon differences in territoriality and differences in behaviour. The behaviour of independent males consists partly of fighting and related activities. This group of behaviour patterns is very rare in satellite males.

This classification was highly correlated with differences in the nuptial plumages. Independent males have predominantly dark or coloured ruffs and head tufts; in general satellite males are white.

Independent males can be further subdivided into resident males and marginal males. Resident males are the owners of small territories or residences. The marginal males on an arena do not possess a residence there,

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I also thank Dr G. W. Johnstone, Drs M. Baars, and Miss Tineke de Boer for their help in the field. Dr Helga Gwinner-Hanke advised and assisted in the breeding of youngs. Mr D. Drenckhahn sent a number of stuffed Ruffs in order to show the distinction between yearlings and adults (cfr. Drenckhahn, 1968). Drs Gré Blokzijl informed me about the technical aspects of film analysis. Members of the Vogeltrekstation, particularly Dr A. C. Perdeck and Mr B. J. Speek, advised and offered their assistance in trapping Ruffs on the arena. Mr J. Holtman's advice and help prevented an extermination of all males on one arena. He and his colleagues also took care for the Ruffs kept in confinement.

For many invaluable discussions I am very greatful to my colleagues. Dr Lidy Hogan-Warburg always managed to save some time for me during her visits to Groningen and to the ethological conferences. Dr J. Reddingius improved on the theoretical approach of this study, and Dr W. van Delden discussed the genetical aspects.

I thank Mr G. Thomas for correcting the english text, Mr L. Hoekstra for preparing the figures, and for typing the final manuscript I thank Mrs H. Lochorn-Hulsebos. I wish to express my thanks to all friends, who helped me in many ways.

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but they may have one on another arena. The status of a resident male may be interchanged with that of a marginal male: resident males may lose their residences, and marginal males are potential possessors.

Satellite males are not territorial. Their behaviour directed towards possessors of residences almost never contains any activity related to fighting. A satellite male makes use of the residences of the territory owners, and often stays together with the possessor on its residence.

A resident male behaves in several ways towards visiting satellites. When a resident male has females on his residence, attacks on satellite males occur relatively often. In many other cases satellite males are accepted by resident males without signs of intolerance.

II. SCOPE OF THIS STUDY

a. Causation of behavioural differences.

The differences in behaviour between resident males, marginal males, and satellites have been interpreted by HOGAN-WARBURG (p. 154) as differences in motivation. Resident males were supposed to have a strong aggressive motivation, but only a weak escape motivation. Marginal males were supposed to have a weak aggressive motivation, but a strong escape motivation. The motivation of satellite males was supposed to be "well balanced" with respect to aggression and escape. The sexual motivation of satellite males was supposed to be relatively high, compared with aggression and escape.

The main line of HOGAN-WARBURG's argument seems to be plausible. However, the starting points for this argument have not been analysed very extensively. These hypotheses were exclusively based on qualitative data, a kind of evidence insufficient for statements on the motivation of the different behaviour patterns. Furthermore no attempt has been made to investigate whether in the Ruff different behavioural mechanisms for the functions of aggression, escape, and sex can really be distinguished. Therefore, it seemed useful to tackle this problem again (Chapter IV) with a more detailed analysis of quantitative data.

b. Ontogenetical basis of the differences.

The differences in behaviour between independent males and satellite males might be controlled genetically and/or environmentally. HOGAN-WARBURG only presented arguments for a genetical control of the differences in behaviour. Recent observations do not entirely support these conclusions. In Chapter V some arguments will be presented for the possibility of environmental control of some of the differences between both groups of males.

c. Functions of behavioural dimorphism.

Independent males and satellite males play different roles in the reproductive system of the Ruff. The role of independent males seems to be very clear: they establish the arena and the residences, taking care of mating places for individuals of this species. The role of satellite males in the whole system is less obvious. HOGAN-WARBURG (p. 217) suggested that "satellite males create the necessary conditions on the residences to enable resident males to attract and stimulate females to crouch for them". She further stated of satellites: "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".

In Black Grouse (KRUIJT, DE VOS & BOSSEMA, 1972), arenas are probably established after cocks have had experience with females on those places. Establishments of territories in this species also seems to be dependent on female experience on those locations. For this reason the chance of female visits on territories is higher than with territory establishment independent of female experience.

In Ruffs it is less clear whether female experience is necessary for territory or arena establishment. It is possible that in this species the satellite males play the role of "link" between owners of mating places and females.

The question as to what extent resident males profit by making use of satellites in order to enlarge their reproductive output has been worked out in Chapter VI.

d. Survival of both behavioural types in a population.

When a balanced polymorphism exists in a Ruff population as HOGAN-WARBURG argued, at least some of the differences between independent males and satellite males have to be genetically determined. Only a few breeding experiments with birds kept in confinement have been done so far, and therefore the results are still disputable. However, it is very probable that there is some genetical control.

Furthermore, when a balanced polymorphism exists there must be a mechanism controlling the relative frequencies of both categories of males within a population. The mechanism HOGAN-WARBURG had in mind, was rather complicated. My data do not fit exactly with her ideas, and therefore a new hypothesis will be presented in Chapter VII.

III. MATERIAL AND METHODS

a. Film analysis.

For this study about 500 meters of 16-mm film of Ruff display on the Dutch island of Schiermonnikoog was used. This film was taken in 1960 and 1961 by Prof. Dr

G. P. BAERENDS, Miss G. J. BLOKZIJL and Mrs A. J. HOGAN-WARBURG. This material has been analysed by means of a projector with a variable speed (1-24 frames/second) and a frame counter. A description with respect to the observation methods on the behaviour of the different animals in this film is presented in Chapter IV.

b. Field observations.

Six arenas in the northern part of the Netherlands have been studied in detail. A number of other arenas were visited only occasionally. This study started in 1967; before that year only some less important observations were carried out. The main part of the data were collected on two arenas near Roderwolde (cfr. HOGAN-WARBURG, p. 114).

These field observations were generally started about April 10; they ended normally about June 10. Most data were collected between half an hour before sunrise to about 8 a.m. Because Ruffs can be very active during the rest of the day, many occasions have been utilized to observe at other hours.

Observations were mostly carried out from a hide of one cubic meter placed approximately 20 meters from the arena; one arena could be observed from my car. On some occasions the hide was placed on a platform, one meter above the ground; near one arena the hide was even placed three meters above the ground surface in order to see the birds moving from one arena to the other.

One year some observations were carried out from a caravan at a distance of about 50 meters from the arena. In that year it was often possible to keep an eye on the arena during the whole day.

For the observations, field glasses (8× 40) and a telescope (40 × 60) were used; for recording behaviour an ordinary watch, a stopwatch, a notebook, a pencil, and a taperecorder were the necessary resources.

IV. STRUCTURE OF THE BEHAVIOUR

A. INTRODUCTION

This part of the paper predominantly deals with the analysis of film material. The film was taken long before this study started and the original purpose was not entirely in accord with its usage in this study. Although almost all aspects of Ruff display were represented in this film, it was difficult to find a suitable method for a quantitative analysis of the behaviour.

In the film it was not possible to recognise all animals individually, so I have not distinguished between individuals. Males and females could be distinguished easily. It was not difficult to decide whether a male was an independent male or a satellite. However, it was not possible to draw a precise distinction between resident males and marginal males. Most resident males could be recognised; all other independent males are not represented in the analysis. The analysis only refers to the behaviour of individuals with an identifiable status.

The majority of shots did not show the whole arena with all birds that were present at that moment. For this reason the analysis was restricted to small groups of 2 or 3 birds, mostly on the same residence. These groups could be composed in different ways; the following compositions occurred frequently enough for a quantitative analysis:

(i) two resident males in close contact (fighting),
(ii) a resident male with a satellite on his residence,
(iii) a resident male with two satellites on his residence,
(iv) a resident male with a female on his residence, and
(v) a resident male with a satellite and a female on his residence.

The durations of the different shots in the film varied tremendously. Shots shorter than 5 seconds (100 frames) were not used. Longer shots containing the earlier mentioned situations have been analysed with a precision of about 0.1 second (2 frames). For this analysis it was useful to divide the whole repertoire of behavioural units in different groups, which are discussed briefly below. The examples mentioned below do not necessarily refer to the Ruff.

(i) *Postures* can be considered as the basic structure of the behaviour. An animal never does nothing, at every moment it shows a posture. When one posture ends, automatically another posture begins. No animal is able to show two postures at the same time. Examples: standing, sitting, *etc.* The other groups of behavioural units are all superimposed on the basic structure of the postures.

(ii) *Locomotion sequences* are regular patterns of repetitions of a simple sequence of movements; owing to this the animal moves from one place to another. A locomotion sequence takes a variable amount of time; different locomotion sequences cannot be shown at the same time by the same animal.

Examples: walking, running, *etc.*

(iii) *Action sequences* are more complicated sequences of movements; repetitions can occur, but the pattern is not necessarily regular. An action sequence takes a variable amount of time; different action sequences can be shown at the same time by the same animal; an action sequence can also be combined with a locomotion sequence.

Examples: eating, preening, *etc.*

(iv) *Actions* are short simple movements. An action takes about a constant amount of time; different actions can be shown at the same time by the same animal; actions can also be combined with action sequences and locomotion sequences.

Examples: pecking, kicking, *etc.*

Furthermore the orientation of the animals, and the distances and angles between them were investigated.

B. DESCRIPTION OF THE BEHAVIOURAL UNITS

The behavioural units are grouped according to the classification in the previous section. It is mentioned briefly to what extent these units are shown by the different categories of individuals. The terminology of HOGAN-WARBURG (p. 200-212) has been followed as much as possible.

1. Postures.

i The Upright (upr — Fig. 1a) is shown predominantly by resident males and females. The body axis points upwards at an angle between 60° and 90° with the horizontal. The neck is stretched vertically upwards. The legs are stretched, the tail is held low, and the wings are folded. In males ruff and head tufts are more or less flattened.

ii Tiptoe (tip — Fig. 1b) is only shown by satellite males. The body axis points upwards at an angle between 45° and 75° with the horizontal. Head and bill point obliquely downwards. Ruff and head tufts are raised in a specific way. The other characters are similar to those of the "upright".

iii The Oblique (obl — Fig. 1c) is shown by resident males, satellite males and females. There are slight differences between these categories. The body axis is obliquely upwards at about a 45° angle with the horizontal. The head extends above the body, the neck is more or less bent, the tail is held in line with the body axis, and covered by folded wings. In males ruff and head tufts are raised in a specific way.

iv Strutting (str — Fig. 1d) is only shown by satellite males. The body axis points obliquely upwards at an angle between 30° and 45° with the horizontal. The neck is held in line with the body axis, the head is turned downwards, and the bill points towards the ground. The legs are bent, the tail is fully spread and held in line with the body axis, the wings are unfolded and held along the sides of the body. Ruff and head tufts are fully expanded.

v The Half Squat (hsq — Fig. 1e) is only shown by males. The body axis is horizontal. The neck is held in line with the body axis, and head and bill point vertically downwards. The male is more or less raised from the ground, the legs are bent, the tail is held in line with the body axis, and the wings may be unfolded to some extent. Ruff and head tufts are raised.

vi The Squat (squ — Fig. 1f) is also only shown by males. The male lies with his belly and breast on the ground, the wings are folded.

Ruff and head tufts are fully expanded. The other characters are equal to those of the "half squat".

vii Crouching (cro — Fig. 1g) is only shown by females. The body axis point downwards. The neck is bent, and head and bill point obliquely downwards. The legs are bent, the tail is held in line with the body axis, and the wings are folded.

viii The Forward (fow — Fig. 1h) is predominantly shown by resident males; females do not show this posture. The body axis is horizontal or pointed downwards. The head is lowered to the same

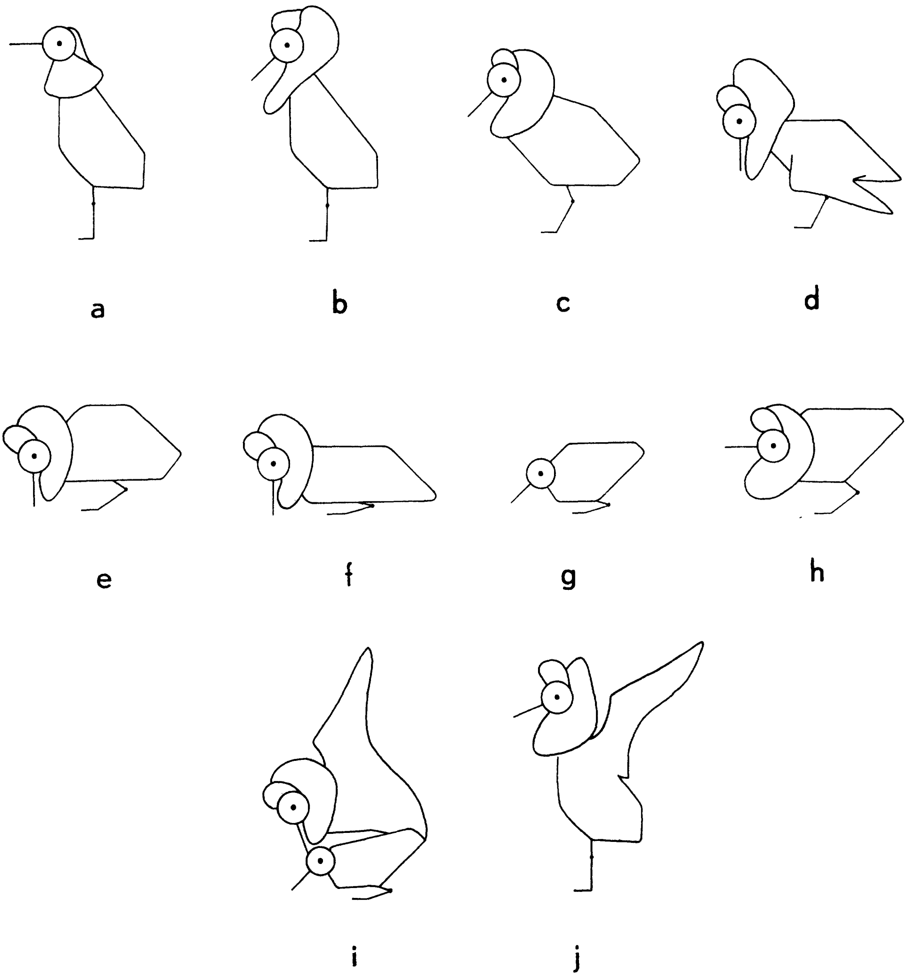

Fig. 1a, Upright; b, Tiptoe; c, Oblique; d, Strutting; e, Half squat; f, Squat; g, Crouching; h, Forward; i, Copulation; j, Wing fluttering.

level as the front of the body, the bill points forwards or slightly downwards. The legs are more or less bent, the tail may be spread, and the wings may be unfolded to some extent. The ruff is fully expanded, and the head tufts are bent forwards.

2. Locomotion sequences.

i Sauntering (sau) is predominantly shown by females and satellite males. The speed of this locomotion sequence is very low.
ii Walking (wal) is also predominantly shown by females and satellite males. The animal moves at a moderate speed.
iii Running (run) is predominantly shown by resident males. The speed of running is relatively high.

3. Action sequences.

i Turning (tur) is predominantly shown by resident males. The animal changes its position or orientation with regard to its surroundings. Turning was not interpreted as a locomotion sequence, due to the irregularity of the pattern.
ii Copulation (cop — Fig. 1i). The mounting act is predominantly shown by males, females may show it occasionally. The body axis is horizontal. The male holds the feathers of the head of the female in his bill. The legs are bent, and the wings spread. The male then bends his tail around the female's tail, beats with his wings, and makes cloacal contact.
iii Tail shaking (tsh) is only shown by females.
iv Wing preening (wpr) is predominantly shown by females.
v Breast preening (bpr) is also predominantly shown by females.

4. Actions.

i Wing fluttering (wfl — Fig. 1j) is only shown by males. The wings are flapped up and down at a moderate speed. The white undersides of the wings are displayed in a very conspicuous way.
ii Wing beating (wbe) is predominantly shown by resident males. The wings are flapped up and down at a high speed. The white undersides of the wings are normally not visible.
iii Bill thrusting (bth) is almost exclusively shown by resident males. The bill may be directed towards other individuals, but it never touches another animal, and remains closed.

iv **Pecking** (pec) is also almost exclusively shown by resident males. The bill is always directed towards another individual, it hits the other animal for a short moment, and may then be opened.

v **Feather pulling** (fpu) is exclusively shown by resident males. This action begins in the same way as pecking, however, during hitting the bill is opened and closed again. During this movement the male grasps some feathers of his opponent, and then pulls with his bill.

vi **Kicking** (kic) is also exclusively shown by resident males. Both feet are used simultaneously in hitting an opponent.

C. RESULTS

1. Order of the postures.

Non-random sequences of behaviour patterns have been used in many studies to investigate the motivational basis of the behaviour (*e.g.*, BAERENDS, BROUWER & WATERBOLK, 1955; WIEPKEMA, 1961). Most of these analyses were based upon behaviour patterns comparable with the action sequences and actions in this study. Other investigations showed that the probability of one behaviour pattern following another was highly dependent on the time interval (without overt activity) between the end of the preceding pattern and the beginning of the following pattern (ISAAC & MARLER, 1963; NELSON, 1964). The predictability of the behaviour was high when the intervals were short. In the present study intervals between postures are always equal to zero: when one posture ends, automatically another posture begins. So an analysis of the temporal patterning of these postures does not have the complication of differences in time intervals.

The order of the postures in resident males, satellite males, and females has been studied. None of these categories of individuals showed essential differences between the orders of postures in the different external situations. Combined data (all situations) are given for resident males satellite males, and females in Table 1.

In resident males the forward may be followed or preceded by all other postures. Transitions between the following postures also occur relatively often: upright and oblique; oblique and half squat; half squat and squat. In satellite males only 4 postures occur frequently enough to be presented here. In this category of individuals, transitions between the following postures occur relatively often: tiptoe and oblique; oblique and half squat; half squat and squat. In females transisitons between the following postures occur relatively often: upright and oblique; oblique and crouching.

In fact the sequence upright-oblique-half squat-squat is not very sur-

TABLE I

Contingency table of posture pairs of resident males

		following					
		upr	obl	hsq	squ	fow	tot
preceding:	upr	—	30	0	0	7	37
	obl	21	—	16	0	49	86
	hsq	1	5	—	42	19	67
	squ	0	0	7	—	27	34
	fow	9	53	57	52	—	171
	tot	31	88	80	94	102	395

Contingency table of posture pairs of satellite males

		following						
		tip	obl	hsq	squ	fow	str	tot
preceding:	tip	—	78	1	1	0	3	83
	obl	64	—	74	0	1	1	140
	hsq	2	62	—	76	0	2	142
	squ	0	2	48	—	2	0	52
	fow	0	1	2	1	—	0	4
	str	1	0	4	2	0	—	7
	tot	67	143	129	80	3	6	428

Contingency table of posture pairs of females

		following			
		upr	obl	cro	tot
preceding:	upr	—	16	0	16
	obl	20	—	11	31
	cro	1	14	—	15
	tot	21	30	11	62

prising, since the shape of oblique is intermediate to the shapes of upright and half squat, and the shape of half squat is intermediate to the shapes of oblique and squat. Thus, the observed relations between the postures might only be due to a physical impossibility of transitions between upright and squat, upright and half squat, and between oblique and squat. If this would be the case, one should expect that two postures occur independently, when separated by the forward. Table 2, however, shows that in resident males with one satellite on their respective residences, triplets in which the forward is preceded and followed by one and the same posture (upr-fow-upr, *etc.*), and triplets in which the first and the last posture can be combined in simple transitions (upr-fow-obl, *etc.*) occur more often than triplets in which the first and the last posture cannot be combined in simple transitions (upr-fow-hsq, *etc.*). From this we may conclude that the relations between the postures are not only caused by a physical impossibility of transitions between some postures.

TABLE 2

Contingency table of posture triplets (forward in the middle) of resident males when they have one satellite on their respective residences

		following				
		upr	obl	hsq	squ	tot
preceding:	upr-fow	1	5	0	0	6
		(0.4)	(2.8)	(1.4)	(1.4)	
	obl-fow	3	16	7	4	30
		(2.2)	(14.2)	(6.8)	(6.8)	
	hsq-fow	0	4	3	2	9
		(0.6)	(4.3)	(2.1)	(2.1)	
	squ-fow	0	2	3	7	12
		(0.8)	(5.7)	(2.7)	(2.7)	
	tot	4	27	13	13	57

	observed	expected	χ^2	probability
first and last posture are equal	27	19.4	3.0	n.s.
first and last posture can be combined	24	20.9	0.5	n.s.
first and last posture cannot be combined	6	16.7	6.9	$p<0.01$

(Expected values in brackets).

2. Similarities in causation between different postures.

The occurrence of transitions between postures is more or less comparable in the different categories of individuals. For instance the transitions between oblique and half squat, and between half squat and squat occur relatively often in both resident males and in satellites, whereas the occurrence of the transition between oblique and squat can be neglected in both categories. However, a number of postures only occur in one category of individuals, so between categories the compositions of the postural repertoires differ to some extent. These differences will be examined in the following paragraphs. Special attention will be paid to the question of how far a posture that only occurs in one category of individuals has a similar causation as another posture that occurs in more categories.

In resident males and females the transition between upright and oblique occurs relatively often. In satellite males the upright is almost never shown. However, tiptoe occurs relatively often and the transition between tiptoe and oblique is very common. This suggests a relationship between tiptoe and upright. Such a relation seems to be very probable because of: (i) the correspondence in form (cfr. Section IV b 1), and (ii) the presumption that tiptoe and upright are elicited by the same external stimuli (particularly by all kinds of alarm situations). This presumption can be supported by the high probability that tiptoe and upright occur simultaneously in different animals in the same group (Table 3). If tiptoe and upright occur independently of each other, one may expect that the total amount of time that both postures occur simultaneously equals:

[(total time spent in tiptoe by satellites) × (total time spent in upright by the other category)] / (total observation time).

The table shows that the observed values are always higher than the expected ones.

The same reasoning can be applied to the similarities between half squat and crouching. In resident males and satellites the transition between half squat and oblique occurs relatively often; in females the transition between crouching and oblique is very common. Furthermore the half squat and crouching correspond in form in many details. However, although both postures tend to occur simultaneously, in this case one cannot conclude that they are elicited by the same external stimuli, since male and female react in a special way to each other prior to copulation. Nevertheless the causal relationship between half squat and crouching is indicated by the following finding. Females which show long bouts of crouching with turning without being mounted by a male, may show mounting behaviour with other females. This is comparable with the behaviour of males prior to copulation. They show bouts of half squat combined with turning.

Strutting did not occur very often in the film, so it is difficult to study the relations of this posture in detail. Transitions between strutting and tiptoe occurred relatively often, transitions between strutting and half squat were also relatively common. These findings suggest some relationship with the oblique. The shapes of strutting and oblique correspond to some extent. However, strutting and oblique are normally not performed in the same situation, furthermore both postures are shown by one and the same category of individuals (satellites). Possibly strutting and oblique are more or less similar with respect to the internal organisation of the behaviour.

3. A model of the behaviour.

The order of the postures and the suggested similarities between postures are summarized in Figure 2. The whole repertoire of postures is represented by a square. Largely similar postures are represented by one and the same area within the square. Postures between which transitions occur frequently are represented by adjacent areas.

The figure can be considered as a simple description of the correlations between the postures. Since correlations may point to common causal factors, we may expect that the causations of two adjacent postures are more similar than the causations of two non adjacent postures.

One might imagine that the appearance of the different postures depends on the values of two variables. All possible values of the one variable can be plotted along the horizontal axis (H) in Figure 2, the values of the other variable along the vertical (V). It is obvious that the appearance of one particular posture can be caused by each of a large number of combinations of values.

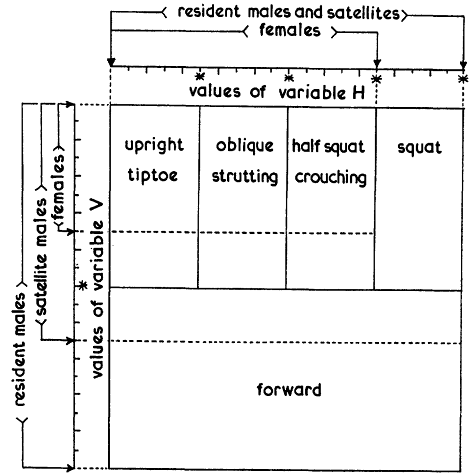

Fig. 2. Order of the postures and similarities. A model of the behaviour. * threshold values.

TABLE 3

Time in seconds that tiptoe of satellite males was observed simultaneously with the upright of another category

situation:	other category:	observed:	expected:
res + 1 sat	res	37.4	15.4
res + 2 sat	res	9.4	2.1
res + sat + fem	fem	10.7	4.5

Both values are supposed to be determined by external and internal factors. A change in the environment might bring on changes in the values of the variables. Gradual changes in the values of both variables result in a normal sequence of postures. The forward — non forward transition must be caused by the crossing of a threshold value of variable V, the other transitions are due to changes in the values of variable H.

If both values change independently the probability of a forward — non forward transition should be constant at all values of variable H. Furthermore the probabilities of the display of upright or tiptoe, oblique or strutting, half squat or crouching, and of the display of the squat should be proportional to the probabilities of the underlying values of variable H. In other words the frequencies of transitions between forward and each of the other postures should be proportional to the percentages of time that each of these other postures were displayed. Table 4 shows that this is not the case for the combined data of resident males ($X^2 = 91.1$, $df = 3$, $p < 0.01$). Transitions between oblique and forward occur more often than should be expected, transitions between squat and forward less often. Thus, both variables do not behave independently.

The behavioural differences between resident males, satellite males and females can be ascribed to differences in the range of both variables. A considerable part of the behaviour of resident males consists of the forward. This implies that in resident males the values on the lower part of the vertical axis (V) occur rather often. In satellites this forward is seldom shown, which suggests that the range of variable V is smaller than is the case with resident males. The forward is completely absent in females; for that reason the range of variable V is probably smallest in this category of individuals.

TABLE 4

Relation between frequencies of transitions between forward and the other postures, and the percentages of time that these other postures were displayed in resident males

posture	total duration in seconds	number of transitions observed	expected	X^2	probability
upright	60.5	16	13	0.7	non sign.
oblique	221.6	102	47	64.4	$p < 0.01$
half squat	347.3	76	74	0.1	non sign.
squat	655.5	79	139	25.9	$p < 0.01$

The squat is also absent in females, which suggests that the range of variable H is smallest in females too. In Figure 2 the approximate ranges of the variables are given for the different categories of individuals.

The other behavioural units are superimposed on the postures. In the following sections (IVc 4-6) it will be shown that these units do not occur randomly, most of them being strongly associated with one or a few postures. These relations between postures and other behavioural units can be interpreted as correspondences in their causations. The appearance of these other units is probably also largely determined by the two variables mentioned earlier. Thus, within the square we can roughly indicate areas with high probabilities of these other units.

It was assumed that for every behavioural unit only one area could be indicated. Within such an area the probability of appearance of the unit is highest; close to the area the probability is low, and at a large distance very low.

The areas, corresponding with different behavioural units, have been indicated in several ways: shape and size can be different. Actions were always represented by circles. In all other cases shape and size roughly give information about the extensiveness of the areas with high probabilities.

4. Locomotion sequences.

The frequencies and the percentages of the total observation time of the different locomotion patterns for the different categories of individuals are given in Table 5. Sauntering and walking are shown by resident males, satellite males, and females. The frequency of sauntering is highest in satellite males and females. Walking also occurs most often in satellites and females. Running is almost exclusively shown by resident males.

TABLE 5

Locomotion in the different categories of individuals

	frequency/1000 sec.			percentage of the total time		
	res	sat	fem	res	sat	fem
sauntering	3	13	15	0.4%	2.1%	2.0%
walking	16	26	19	1.5%	2.4%	3.4%
running	6	1	0	0.3%	0.1%	0.0%

Table 6 shows to what extent the different locomotion patterns are superimposed on the postures. Sauntering occurs very often during strutting, less often during upright, tiptoe, half squat, oblique, and seldom during forward. Walking occurs relatively often during upright, tiptoe, oblique, and seldom during half squat and strutting. Running occurs relatively often during forward, and seldom during oblique and tiptoe.

It is possible now to indicate the locomotion sequences in Figure 3. Sauntering is represented by a long rectangle through upright, oblique, and half squat, at a relatively large distance from forward. Walking is represented by a rectangle through upright, oblique, and a part of half squat, at a relatively short distance from forward. Running is represented by a rectangle in forward, relatively close to oblique and upright.

5. Action sequences.

The percentages of the total observation time of turning, tail shaking, wing preening, and breast preening, and the frequency of turning for the different categories of individuals are given in Table 7. Turning is predominantly shown by resident males. Tail shaking is exclusively shown by females, and breast preening and particularly wing preening are almost exclusively shown by females.

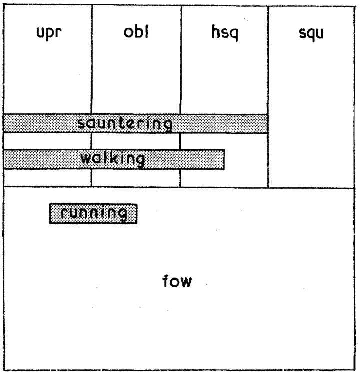

Fig. 3. Locomotion sequences.

TABLE 6

Distribution of locomotion over postures

	percentage of the total duration of the posture			
resident males	upr	obl	hsq	fow
sauntering	0.7%	0.2%	1.9%	0.2%
walking	1.3%	4.0%	0.7%	2.6%
running	0.0%	0.5%	0.0%	0.9%
satellite males	tip	obl	hsq	str
sauntering	3.4%	2.3%	2.8%	20.6%
walking	6.8%	2.6%	1.1%	0.7%
running	0.3%	0.0%	0.0%	0.0%
females	upr	obl		
sauntering	3.2%	2.0%		
walking	4.1%	3.8%		

Table 8 shows to what extent these action sequences are superimposed on the different postures. Turning occurs very often during forward, less often during half squat and crouching, and seldom during upright, tiptoe, and oblique. Tail shaking occurs exclusively during oblique. Wing preening occurs often during oblique, and seldom during upright. Breast preening occurs almost equally often during oblique and upright.

TABLE 7

Action sequences in the different categories of individuals

	frequency/1000 sec.			percentage of the total time		
	res	sat	fem	res	sat	fem
turning	94	31	15	11.3%	2.6%	1.0%
tail shaking				0.0%	0.0%	1.9%
wing preening				0.1%	0.2%	14.3%
breast preening				0.7%	0.7%	8.1%

TABLE 8

Distribution of action sequences over postures

	percentage of the total duration of the posture			
resident males	upr	obl	hsq	fow
turning	3.8%	2.8%	6.0%	30.2%
tail shaking	—	—	—	—
wing preening	0.0%	0.9%	0.0%	0.0%
breast preening	0.0%	6.3%	0.0%	0.0%
satellite males	tip	obl	hsq	fow
turning	1.1%	3.5%	11.9%	30.3%
tail shaking	—	—	—	—
wing preening	0.0%	0.9%	0.0%	0.0%
breast preening	2.5%	0.3%	0.0%	0.0%
females	upr	obl	cro	
turning	0.0%	0.1%	10.0%	
tail shaking	0.0%	2.5%	0.0%	
wing preening	6.5%	18.1%	0.0%	
breast preening	10.3%	10.6%	0.0%	

These action sequences can be drawn as in **Figure** 4. Turning is represented by a large triangle with its base in forward and its top in half squat. Since in females the range of variable V is restricted to the upper part of the vertical axis (cfr. Fig. 2), we can easily place the different preening sequences. Tail shaking, which only occurs in females, is represented by a rectangle in the highest part of oblique. Wing preening, occurring almost exclusively in females, is represented by a rectangle, just below tail shaking, with its main part in oblique, and a smaller part in upright. Breast preening, which occurs also in males, is represented by a rectangle below wing preening; one half of it is drawn in oblique, and the other half in upright.

Copulation and mounting is always superimposed on half squat. Furthermore it resembles strutting, and is generally preceded by turning. Therefore this action sequence is represented by a rectangle in the half squat, close to strutting, and overlapping the top of the turning triangle.

6. Actions.

Wing fluttering occurs in resident males and satellites; wing beating, bill thrusting, pecking, feather pulling, and kicking are almost exclusively shown by resident males.

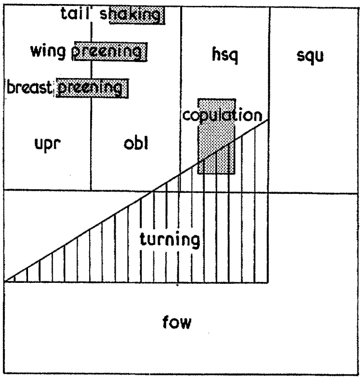

Fig. 4. Action sequences.

Table 9 shows to what extent the different actions are superimposed on the different postures. Wing fluttering occurs almost exclusively during upright and tiptoe. It is seldom shown during oblique, strutting, and forward. Wing beating occurs most often during copulation, and less often during locomotion, oblique, half squat, and forward. Bill thrusting occurs more often during forward and upright than during oblique and turning. Pecking and feather pulling occur almost exclusively during forward and turning.

Wing fluttering, wing beating, and bill thrusting can be drawn easily in Figure 5. Wing fluttering is represented by a circle with its main part in upright, and a smaller part in oblique, relatively close to forward. Wing beating is represented by a circle with one third in half squat, one third in oblique, and one third in forward. Bill thrusting is represented by a circle with one half in upright and one half in forward, relatively close to oblique.

TABLE 9

Distribution of actions over the postures

	frequency/1000 seconds of the posture or other unit						
resident males	upr	obl	hsq	fow	tur	cop	loc
wing fluttering	73	3	0	1	0	0	0
wing beating	0	4	4	3	0	43	13
bill thrusting	8	3	0	9	4	0	0
pec & fpu	0	1	0	22	8	0	0
satellite males	tip	obl	str				
wing fluttering	29	1	6				

For the determination of the locations of pecking, feather pulling, and kicking additional data have been used. These actions occur very often during fights between resident males. In such situations it could be shown that during pecking, feather pulling, and kicking the orientation of the resident male and the distance up to the other individual were largely similar to orientation and distance during wing beating. During bill thrusting these aspects of the behaviour were somewhat different (Table 10). The temporal distributions of wing beating, feather pulling, and kicking (Table 11) are strongly correlated. An analysis of the order in which the different behavioural units were shown during these fighting situations also proved that wing beating occurred more often in combination with feather pulling and kicking, than with pecking (Table 12). Feather pulling and kicking were almost exclusively preceded and followed by wing beating, while pecking was only followed frequently by wing beating.

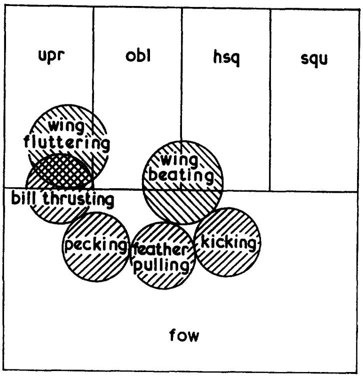

Fig. 5. Actions.

TABLE 10

Orientation and distance during five actions (fighting situations)

	orientation			distance		
	head	side	back	zero	some	long
wing beating	88%	4%	8%	92%	6%	2%
bill thrusting	67%	33%	0%	0%	17%	83%
pecking	99%	1%	0%	98%	2%	0%
feather pulling	99%	1%	0%	99%	1%	0%
kicking	99%	1%	0%	99%	1%	0%

orientation: head = head towards the opponent, side = side towards the opponent, back = back towards the opponent.

distance: zero = bodily contact between both opponents, some = both opponents at the same residence, long = both opponents at different residences.

TABLE 11

Relations in the temporal distribution of five actions (fighting situations)

		mean number of actions per 100 seconds			
wing beats per second	number of seconds	bth	pec	fpu	kic
0	42	14 ↑	12	2	0
1	28	7	46	0	11
2	55	2	40	13	27
3	53	4	57	25	30
4	66	1	59	33	70
5	41	0	51	51	83
6/8	31	0	35	51 ↓	65 ↓
pecking per second	number of seconds	fpu	kic		
0	181	33 ↑	40		
1	129	16	45		
2	6	0	66		
feather pulling per second	number of seconds	pec	kic		
0	242	50 ↑	31		
1	68	28	78		
2	6	17	117 ↓		
kicking per second	number of seconds	pec	fpu		
0	195	41	11		
1	108	54	45		
2	13	31	69 ↓		

With respect to their shapes bill thrusting, pecking, and feather pulling can be interpreted as three different intensities of one and the same movement. Bill thrusting is considered as the lowest intensity, feather pulling as the highest. For this reason bill thrusting, pecking, and feather pulling are represented as three circles on roughly one line. The circle of feather pulling is placed very close to wing beating (Fig. 5).

It is possible now to indicate all behavioural units in Figure 6. The degree of community of the causation of the different units is reflected by overlap (*e.g.* turning and pecking). The causations of units at short distances differ slightly (*e.g.* turning and bill thrusting). The causations of units at large distances are largely different (*e.g.* turning and tail shaking).

7. External stimuli.

The external situation influences the composition of the behaviour of the different categories of individuals. In the film, groups of individuals

TABLE 12

Order of five actions during fighting

following:

		wbe	bth	pec	fpu	kic	other	total
preceding:	wbe	511 — (575)	1 — (5)	82 = (80)	71 + (48)	124 + (84)	125	914
	bth	3 = (4)	1 + (0)	1 = (1)	0 = (0)	0 = (1)	2	7
	pec	125 + (84)	0 = (1)	0 — (12)	1 — (7)	5 — (12)	3	134
	fpu	74 + (49)	0 = (0)	0 — (7)	0 — (4)	4 = (7)	0	78
	kic	127 + (84)	0 = (1)	2 — (12)	2 — (7)	0 — (12)	3	134
	other	70	6	42	2	0	60	180
	total	910	8	127	76	133	193	1447

(maximum interval = 0.5 seconds).

The observed values are given in the upper parts of the squares, the expected values (in brackets) in the lower parts. A "=" indicates no significant difference (X^2 tests, df = 1; or Poisson distribution when "expected" $\leqslant 5$), a "+" indicates that the observed value is significantly higher, and a "—" that the observed value is significantly lower ($p < 0.05$).

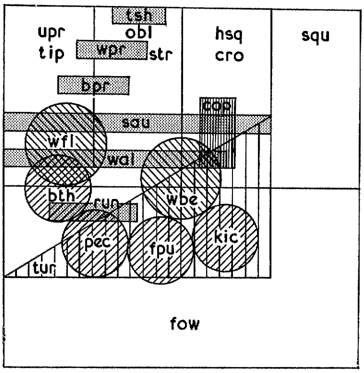

Fig. 6. The whole repertoire of behavioural units.

TABLE 13

Frequencies (per 1000 seconds) and percentages of the time of the postures in different situations

situation:		*r*+s	*r*+s+s	*r*+f	*r*+s+f	*s*+r	*s*+r+s	*s*+r+f	*f*+r	*f*+r+s
upr/tip	*fr*	29	24	0	0	38	66	23	32	18
	%	5	3	0	0	29	19	7	16	22
obl/str	fr	70	52	9	9	77	127	46	54	32
	%	20	4	2	1	25	18	14	71	75
hsq/cro	fr	32	44	47	43	74	105	65	22	14
	%	18	14	24	15	9	22	7	14	3
squ	fr	30	32	38	45	35	44	42	0	0
	%	23	22	61	49	33	41	71	0	0
fow	fr	87	86	34	67	0	0	0	0	0
	%	34	57	13	34	0	0	0	0	0

(the behaviour is shown by the first mentioned individual).

with five different compositions have been studied in detail (Section IVa). Resident males could be observed in five different situations, satellite males in three situations, and females in two situations.

The occurrence of the different postures is strongly associated with the situation. This is shown in Table 13: both the percentage of the time involved as well as the frequencies differ greatly in the different situations. The data about fights between resident males are not presented, because the identification of the postures was rather doubtful in this situation. The observed differences in behaviour can be partly attributed to an influence of external stimuli on the ranges of both variables in the model.

The behaviour of resident males is strongly influenced by satellites. An additional satellite (comparison between *r* + s and *r* + s +s, and between *r* + f and *r* +s + f) increases the percentage of forward. This implies that the values on the lower part of the vertical axis (V, Figure 2) become more likely. The influence of an additional female (comparison between *r* + s and *r* + s + f) is restricted to the value of variable H, because the percentage of forward does not change and the percentage of squat increases.

Satellite males are influenced in their behaviour by the presence of other satellites (comparison between *s* + r and *s* + r + s). An additional satellite increases the percentages of half squat and squat, and decreases the percentages of tiptoe and oblique, and thus has an influence on the value of variable H. The value of this variable is also influenced by the presence of a female (comparison between *s* + r and *s* + r +f). An additional female increases the percentage of squat and decreases the percentages of tiptoe and oblique.

The behaviour of females is somewhat influenced by the presence of satellites. An additional satellite (comparison between *f* + r and *f* + r + s) decreases the percentage of crouching, and thus has an influence on the value of variable H.

Influences on the value of variable V could not be established in satellite males and females, since the percentage of forward was very low or equal to zero in these categories of individuals. So we cannot decide whether the same external stimuli (*e.g.* an additional satellite male) have similar effects on the range of variable V in the different categories.

The range of variable H changes in about the same direction in both resident males and satellites after changes in the external situation. An additional satellite causes a moderate increase of the percentages of half squat and squat, and a decrease of the percentages of upright (or tiptoe) and oblique; an additional female causes a sharp rise of the percentage of squat in both categories of individuals. The change of the range of variable H in females, however, is different from that in resident and satellite males: an additional satellite causes less crouching in females, thus the values on the right part of the horizontal axis become less likely.

The occurrence of the other behavioural units is also associated with the situation (Table 14). The differences in their frequencies and percentages of time involved between the different situations are compatible with the

TABLE 14

Frequencies (per 1000 seconds) and percentages of the time of the other behavioural units in different situations

situation:		*r*+s	*r*+s+s	*r*+f	*r*+s+f	*s*+r	*s*+r+s	*s*+r+f	*f*+r	*f*+r+s
locomot.	fr	21	15	37	21	38	41	31	37	28
	%	2	2	3	3	5	4	4	6	4
tur	fr	98	103	62	80	24	36	18	20	0
	%	12	13	9	10	3	3	1	2	0
cop	fr	—	—	7	—	—	—	—	—	—
	%	—	—	7	—	—	—	—	—	—
tsh	fr	—	—	—	—	—	—	—	22	14
	%	—	—	—	—	—	—	—	2	2
wpr	fr	—	—	—	—	—	—	—	80	80
	%	—	—	—	—	—	—	—	16	11
bpr	fr	—	—	—	—	—	—	—	37	66
	%	—	—	—	—	—	—	—	7	13
wfl	fr	54	10	—	—	97	47	—	—	—
wbe	fr	6	25	52	28	4	5	0	34	33
bth	fr	47	25	12	18	—	—	—	—	—
pec/fpu	fr	44	309	0	108	—	—	—	—	—

(the behaviour is shown by the first mentioned individual).

previously stated influences of the external stimuli on the ranges of both variables.

The external situations above appear as large complexes of different stimuli in which the various components tend to gradually appear, disappear or change in intensity. Changes in the values of both variables coincide with this. Abrupt changes in these values are not needed for the proper response of the individual to the various stimuli in most social relations. As opposed to this, we may expect that the proper reaction on a sudden stimulus (*e.g.* the appearance of a predator) needs a very rapid change in the values of both variables. However, it is likely that such rapid changes do not occur. Qualitative field observations on sudden fright stimuli (human beings departing from a hide, birds of prey, airplanes, *etc.*) suggest that the behaviour, shown by the individual prior to such a stimulus, largely determines the reaction. In almost all cases the individuals flew away from the arena after upright and oblique. After half squat and squat, however, the individuals mostly lay flat on the ground. After forward both reactions occurred. Since flying away is always preceded by the upright posture, and lying flat is largely similar (with respect to the shape of it) to the squat, we must conclude that even after abrupt changes in the external situation transitions between non-adjacent postures only seldom occur. So, the values of both variables are not strongly affected by these abrupt changes.

D. DISCUSSION

1. Significance of the model.

In this chapter I have shown that the behavioural units investigated in resident males, satellites, and females are closely bound up with each other. Both the transitions between postures (Section IVc 1), and the simultaneous displays of postures and other units (Sections IVc 4-6) do not occur randomly.

What would be the simplest model to explain this distribution? It is perspicuous to try the first possiblity that all correlations, visualized in Figure 6, are caused by the external situations, consisting each of a number of coincident stimuli which affect more or less simultaneously different internal causal mechanisms. If this was the case, one would expect the correlations between the behavioural units not to be the same in the different external situations. It has been stated however, that the order of the postures is largely similar in all external situations investigated (Section IVc 1). Furthermore, postures and other behavioural units tend to occur together irrespective of the external situation (Section IVc 7). We must therefore conclude that the observed relations between the behavioural units must at least be partly ascribed to internal associations. This conclusion can be further supported by the findings that (i) the relations between the behavioural units are similar in the different categories of individuals (Sections IVc 1-6), and (ii) the reaction to fright stimuli is correlated with the behaviour shown prior to such a stimulus (Section IVc 7). Consequently the values of the two hypothetical variables (Section IVc 3), by which we could describe the order of the postures, and the relations between postures and other behavioural units, are not exclusively defined by the external situation.

Are these variables sufficient to explain the incidence of all behavioural elements? I have shown (Section IVc 3) that the incidence of postures can almost entirely be described on the basis of the values of both variables. The incidence of the other behavioural units, however, must also depend on additional factors, since the corresponding areas in the model only imply that the probability of appearance is high, but not in most cases equal to 100%. This implies that we need more causal factors for the explanation of the causation of these other units. These factors are presumably connected with the external situation, since locomotion sequences, action sequences, and actions are closely bound up with particular external stimuli, namely position and behaviour of the other individuals in the neighbourhood. Such external stimuli must play an important role in directing the behaviour. We may assume that the strength of the external stimulus (weak, normal, or strong), which is needed to elicit a given behavioural unit, is determined by the values of both variables. If these values correspond with a given area in the model (Figures 3-5), it is presumed that the normal strength of the external stimulus required is sufficient to elicit the behavioural unit in question.

Which factors affect the values of both variables? I have shown (Section IVc 7) that the range of both variables is influenced by the external situation. A sudden change in the stimulus situation, however, does not cause an abrupt change in the values of both variables (Section IVc 7). So, the value of a variable also strongly depends on the preceding values, and thus on previous external stimuli. The last mentioned dependency may be a consequence of the nature of both variables. Furthermore, the ranges of both variables are closely associated with the status of the individual (Section IVc 3). This implies that the value of a variable must be influenced by one or more internal factors.

The causal relations discussed above can be summarized in a diagram (Figure 7). The occurrence of all postures (P) is controlled by a combination of both variables (H and V). The only exception is the forward

(F), which is independent of the value of H. The occurrence of all other behavioural units (O: locomotion sequences, action sequences, and actions) also depends on additional causal mechanisms (S), of which each is controlled by one or more particular external stimuli (E). The values of both variables (H and V) are controlled by a large number of external stimuli (E), and by one or more internal factors (I).

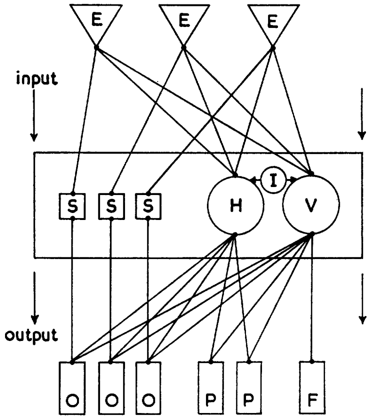

Fig. 7. Causal relations (explanation see text).

H and V can be regarded as "intervening variables" (cfr. TOLMAN, 1932), or "drives": they are controlled by a large number of stimuli (independent variables), and they direct the behavioural output (dependent variables). These drives, however, do not refer to complexes of behavioural units that serve one function for survival (aggression, flight, sex, *etc.*). Such complexes only appear at distinctive combinations of values of both variables. Behaviour with an aggressive function, such as forward, kicking, feather pulling, and pecking is localized in only one area in the model (Figure 8: A). This implies that behaviour with an aggressive function can also be regarded as one causal complex of behavioural units. Behaviour with a sexual function (squat, half squat, crouching, and copulation) also belongs to one causal complex (S). Nevertheless behaviour with a protective function (flying away, lying flat; after fights: bill thrusting and running) can occur respectively in three greatly differing combinations of values (Figure 8: P1, P2, P3), in other words, protective behaviour can appear at different internal states of the animal.

The drive concept, as used by ethologists (*e.g.* TINBERGEN, 1952; BASTOCK *et al.*, 1954; HEILIGENBERG, 1964), is for the greater part (functions for survival, control of a limited number of behavioural units, incompatibility of drives, *etc.*) applicable to the causal complexes indicated in Figure 8 (A, S, P1, P2, P3). The present model emphasizes that all of these complexes may be the consequence of one and the same causal mechanism, in this case the values of only two variables (H and V).

I wish to close this section with some comments on the methods used in this chapter. They may be less impressive from the mathematical point of view, than elaborate methods like factor analysis, *etc.* At the initial stage of this study, however, I tried to employ factor analysis. With that method the results appeared to be utterly dissimilar under different external situations. Thus, the results were strongly influenced by external stimuli, and therefore not very useful to elucidate the internal relations between the behaviour units.

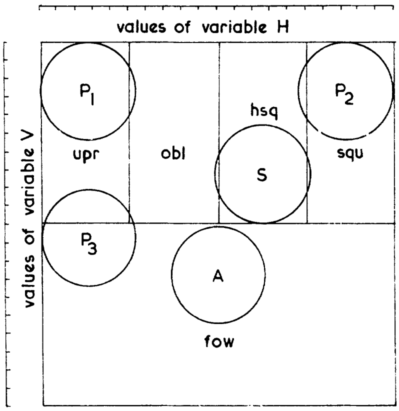

Fig. 8. Causation and function of the behaviour. A = behaviour in aggressive situations; S = behaviour in sexual situations; P1 = protective behaviour (flying away); P2 = protective behaviour (lying flat); P3 = protective behaviour (after fights).

In order to minimize the interference between internal and external factors, I analysed each of a large number of behavioural aspects separately by means of the methods presented in this chapter. Some of these aspects (viz. order of postures, and relations between postures and other behavioural units) remained constant or fairly constant during all kinds of external situations investigated. Such evidence enables us to speculate about the internal organisation of the behaviour.

Our model cannot be considered as the only possible explanation for the observed relations. We must realize that it is almost exclusively based upon the order of postures. For the explanation of this order in resident males we needed at least two variables; for the explanation in satellites and females at least one. Because of the similarities in the behaviour between the different categories of individuals, it was supposed that two variables could be distinguished in all categories. This idea was supported by the relations observed between postures and other behavioural units. Thus, the two variables-hypothesis must be considered as one of the most (possibly the most) perspicuous explanation for the causation of the behaviour in the Ruff. Since both variables seem to be more abstract than for instance aggression, flight, and sex (in a causal sense), we must be aware of the danger of losing sight of the living animal. On the other hand, their abstract nature protects us from misapplications in other animals.

2. Behavioural differences between the categories.

The data presented in this chapter suggest that all categories are potentially able to show all behaviour patterns. The behaviour in the distinct categories only differs with respect to the frequencies and the durations of the elements; in a few cases modifications of basic patterns (*e.g.* crouching and half squat) are involved. The behaviour of resident males contains a number of units that seldom occur in the other categories of individuals; female behaviour contains units, that seldom occur in satellites and resident males. The behaviour of satellite males may be considered intermediate; it contains both elements of the behaviour of territory owners, and elements of female behaviour. The only category-specific patterns (tiptoe and strutting) are supposed to be largely similar to non-category-specific patterns (upright and oblique).

Untypical sexual behaviour, viz. female behaviour performed by males, and male behaviour performed by females, occurs in many animal species (cfr. VAN DEN ASSEM, 1967; BAERENDS & BAERENDS-VAN ROON, 1960 BARRAUD, 1955; MORRIS, 1952, 1954, 1955, 1958; WIEPKEMA, 1961). The work of VAN DEN ASSEM (*l.c.*) in particular shows that untypical sexual behaviour plays a role in the reproductive success of individuals. Males of the three-spined stickleback (*Gasterosteus aculeatus* L.) sometimes perform female behaviour, and consequently steal fertilizations of clutches of eggs from neighbouring males. This behaviour is highly comparable with the behaviour of satellites.

We shall now consider which factors may play a role in the control of satellite behaviour. First, the difference in plumages between the dark independent males and the mainly white satellites may be a very important factor. In the following chapter (V) it will be shown that in many cases the relation between its own plumage and that of the other males on an arena determines the status of an individual. Besides this, correlated genetical factors may directly influence the behaviour. Second, the lack of a territory may play a role. Two cases of a "satellite", which temporarily defended a residence, have been observed (cfr. Chapter V). The behaviour shown by these "satellites" did not differ from normal resident male behaviour. Third, we must consider the possible effect of the behaviour of resident males on satellites. A satellite male present on a residence gets no opportunity to display towards females, since this would evoke an attack of the resident male. Moreover, satellite males are seldom tolerated on a residence with one or more females (cfr. Chapter VI). We should consider whether these aspects of the behaviour of resident males have a modifying influence on the display of satellites. Furthermore, the behaviour of resident males towards satellites contains many features (squat, half squat, turning, *etc.*) which also occur in the behaviour towards females. Such behavioural characteristics are not shown towards other independent males. Therefore, satellite behaviour is also possibly controlled by stimuli which normally affect sexual behaviour in females.

Thus, the divergent behaviour of satellite males may be influenced by three factors:

(i) the light plumages and correlated genetical factors which also directly influence the behaviour,
(ii) the lack of a territory, and
(iii) the behaviour of resident males towards satellites.

The first factor, which will be discussed in the following chapter (V), is probably the most important one. The other factors may be consequences of this first one: (a) the light plumages of satellites probably influence the behaviour of resident males, and (b) the ability to use the territories of other males, prevents satellites from getting one.

V. ONTOGENETICAL BASIS OF THE DIFFERENCES

Hogan-Warburg (p. 213-214) presented arguments for the hypothesis that the behavioural differences between independent males and satellite males are controlled by a set of genes, which is closely linked with the set of genes controlling the plumage differences. She rejected the possibility of an influence of the environment on the differentiation process. In opposition to this I obtained some support for the hypothesis that in addition to genetical factors the environment also plays a role. The underlying arguments will be presented in the following paragraphs:

(a) the status of some individuals (particularly young ones) is not absolutely constant, and
(b) the status of an individual is associated with its own plumage colour *and* with the plumage of the other individuals present on the same arena.

a. Constancy of the status of an individual.

The classification of male Ruffs was based upon two criteria: "(1) differences in territoriality and attachment to the lek; and (2) differences in behaviour patterns that serve communication among the birds" (HOGAN-WARBURG, p. 129). "The status between resident males and marginal males is interchangeable (p. 130); "transformations from satellite male to independent male have never been observed", although "it may very occasionally occur that a male shows behaviour that contains features characteristic of another group" (p. 133).

My data fully agreed with this, until I observed a satellite male, which adopted the role of resident male for a few days.

Although empty residences are seldom visited by satellite males, this "satellite" payed much longer visits to a distinct residence during a 3 days absence of the resident male, than before that time. On the first day neighbouring resident males sometimes entered the residence with the "satellite", and behaved as if they were on their own residence. On those occasions the "satellite" displayed normal satellite behaviour. During the second and third day the "satellite" did not tolerate resident males on "his" residence, where he was about equally often present as the resident males on their residences; he did not show satellite behaviour during these days. When the previous possessor returned, the "satellite" and the resident male started a very heavy fight. After some minutes the "satellite" turned out to be the loser; he left the residence, and behaved like a satellite on other residences. About half an hour later he returned to his former spot, where he was tolerated as a satellite by the possessor.

This observation shows that the differences between independent males and satellites are not as constant as HOGAN-WARBURG suggested. Transformations from satellite male to independent male are possible, at least for a few days.

The results of the previous chapter (IV) throw some additional light on this phenomenon. I indicated there, that the behavioural repertoires of independent males and satellite males are composed of the same elements. Only the frequency distributions for the occurrence of these elements (thus quantitative properties) differed between both categories. Moreover, the frequencies of these elements were dependent on the external situation. Hence, it is likely that exceptional circumstances can result in uncharacteristic behaviour. Observations on a caged satellite male give some support for this hypothesis.

During the reproductive period one "satellite" male displayed normal resident behaviour, when put together with females and separated from resident males. He showed a strong preference for only one spot in the cage and visited other sites almost exclusively during foraging trips. He did not pursue females, encounters with females normally took place on the preferred spot. During the same season the

> male exhibited normal satellite behaviour after an introduction of resident males in the same cage. The "satellite" now entered "residences" of resident males and followed females to all places of the cage. The "satellite" no longer showed a preference for a particular spot in the cage. Thus, the presence of resident males appeared to be a very important condition in eliciting satellite behaviour.

The above mentioned cases of changes of status refer to males more than one year old. In yearlings (recognizable by gray legs) changes of status can occur very often. I observed at least 15 of these males in which the status was doubtful. They exhibited components of both kinds of behaviour during one and the same visit to the arena. Five of them had partly developed nuptial plumages, the other ten still lacked such a plumage.

With respect to these young males HOGAN-WARBURG only once observed components of both kinds of behaviour in the same individual, although she spent about the same time in observation as I did. This phenomenon, however, can be easily overlooked since many of these males cannot be recognized individually and they may visit the arena in large groups, mostly staying for only a few minutes.

b. Association between plumage and status.

Extreme individual diversity in the male nuptial plumage is characteristic of the Ruff. The differences in behaviour between independent males and satellite males are associated with differences in the plumage. Some plumage types occur exclusively in satellites (plain white ruff and head tufts; plain white ruff and white head tufts with any pattern; white ruff with any pattern and plain white head tufts). In the following paragraphs the term "*satellite plumages*" will be used for this group. Other plumage types exclusively occur in independent males (any ruff and black head tufts), they will be described as "*independent plumages*". The remaining group of plumage types can be found in both categories of males ("*untypical plumages*"). This classification differs from that used by HOGAN-WARBURG, who classified predominantly dark satellites and predominantly light independent males as anomalous plumages. In general dark males have the independent status, and light coloured males the satellite status.

In a large proportion of males, the behavioural phenotype and the type of plumage are apparently determined by common or correlated causal factors (satellite and independent plumages). In the other males this is not the case: at least one phenotypical feature must be influenced by factors that do not affect the other feature. These factors can be sought in the genotype of an individual and/or in the environment to which it is subject. In the previous section (Va) I presented some evidence for environmental influences. In this section I want to discuss a special case of such influences, viz. to what extent the status of individuals with untypical plumages depends on the relative frequencies of males with independent and satellite plumages. For reasons of simplicity in the following the term "*dark*" will be used for independent males with independent plumages and satellite males with untypical plumages, while the term "*light*" will describe independent males with untypical plumages and satellite males with satellite plumages.

HOGAN-WARBURG's observations (p. 162) show that in localities where more than 50% of the satellites are dark (Hasselt, Oosterwolde Polder) the proportion of dark independent males is higher than in localities with at most 50% dark satellites (Schiermonnikoog, Roderwolde) (Table 15, $X^2 = 5.9$, df = 1, $p < 0.05$).

My own observations reveal the same phenomenon. Both in different localities (Table 16, $X^2 = 5.5$, df = 1, $p < 0.05$) and in one locality during successive seasons (1968-1972; Figure 9) I could demonstrate a relation between "darkness" of satellite males and of resident males[1]).

TABLE 15

Relation between plumage colours of independent *males and satellites in different localities*

% of satellite males with untypical plumages	Number of independent males with: Independent plumages		Untypical plumages	
> 50% *)	56	(48.9)	29	(36.1)
⩽ 50% **)	20	(27.1)	27	(19.9)

$X^2 = 5.9$, df = 1, $p < 0.05$; (expected values in brackets).
*) Hasselt, O.P., **) Schier, Roder.

TABLE 16

Relation between plumage colours of resident *males and satellites in different localities*

% of satellite males with untypical plumages	Number of independent males with Independent plumages		Untypical plumages	
> 50%	17	(11.7)	7	(12.3)
⩽ 50%	22	(27.3)	34	(28.7)

$X^2 = 5.5$, df = 1, $p < 0.05$; (expected values in brackets).

---

[1]) N.B.: in HOGAN-WARBURG's Table 13 no distinction has been made between resident males and marginal males. For that reason I compared satellites with independent males. My own data are not complete with respect to marginal males, hence my analyses are restricted to satellite and resident males.

Thus, the percentage of dark males can be different in different localities as well as in different seasons; the percentage of dark satellites fluctuates in the same direction as the percentage of dark independent or resident males.

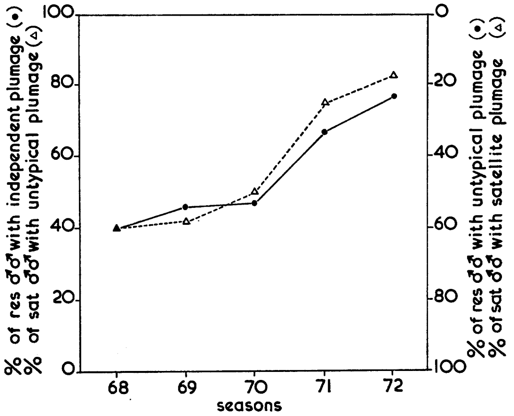

Fig. 9. Relation between plumage colours of *resident* males and satellites in different seasons.

Changes in the percentage of dark males might be due to a high reproductive success of a limited group of males. The reproductive success is taken to be dependent on the copulation frequency. The percentages of resident male's copulations performed by light and dark coloured individuals have been measured during successive seasons (1968-1972) in one locatily. This percentage appeared to be low for dark resident males during the first three years; nevertheless the proportion of dark resident males increased (Figure 10). The percentage of copulations performed by satellite males was very low during these seasons (below 10%). These data cannot be fitted in a simple genetical model. Thus, differential reproduction during previous seasons cannot be the cause of the changes in the percentage of dark males.

The alternative hypothesis presumes that the percentage of dark males is controlled by environmental factors. It is likely that such factors can be found on the arena, since the percentage of dark males can be very different between near-by arenas. So, probably males of all kinds of plumage types are potential visitors of an arena, but only some of them visit an arena for a long period. To sustain this supposition I examined on one arena during two seasons the "tenacity to stay" of individuals of different plumage groups. In the first season (1968) the males were mainly light coloured, in the second one (1971) the males had predominantly dark plumages. It could be demonstrated for resident males that the number of individuals belonging to the "common" plumage group ("dark" on an arena with mainly "dark" males, or "light" on an arena with mainly "light" males) staying more than five days on their residences was higher than that of the "rare" group ("dark" on an arena with mainly "light" males or *vice versa*) (Table 17; $X^2 = 7.2$, df = 1, $p < 0.01$). For satellites of either plumage group the "tenacity to stay" could be averaged. Table 18 shows the mean percentages of time that individuals of either group were present on the arena. In both seasons this percentage was higher in the "common" plumage group. In 1968 the difference between both groups was very small. This was caused by one male of the "rare" plumage group: he was present during 35% of the time. Moreover, this male changed his status (cfr. Section Va). If we discard this male, the percentage of the "rare" plumage group drops far below the percentage of the "common" group (Table 18: "correction").

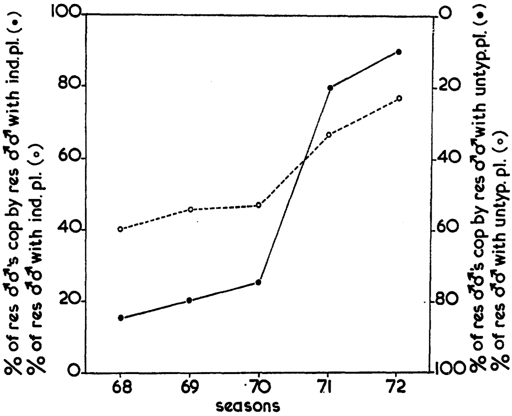

Fig. 10. Relation between plumage colours of *resident* males and copulation frequency.

The above-mentioned data suggest that, depending on the plumage, part of the visiting group to an arena does not stay for a long period. Probably males belonging to the "rare" plumage group are more inclined to migrate towards other arenas than males of the "common" plumage groups. Only two cases of migration of banded independent males are known. Both males belonged to a "rare" plumage group on the arena deserted by them. On the other arena, at a distance of at least 10 kilometres, they settled as part of a "common" plumage group. In addition to the known cases of mortality, 14 banded males belonging to a "rare" plumage group and 15 banded males

TABLE 17

Relation between plumage colour of resident males and duration of staying on a residence

	Number of resident males in:					
	1968, with:		1971, with:		total, with:	
staying on a residence during:	Independent plumage (rare)	Untypical plumage (common)	Independent plumage (common)	Untypical plumage (rare)	Rare plumage	Common plumage
$\geqslant$ 5 days	3	9	9	3	6(10.9)	18(13.1)
$<$ 5 days	6	3	3	8	14(9.1)	6(10.9)

$X^2 = 7.2$, df $= 1$, $p < 0.01$; (expected values in brackets).

of the "common" group disappeared from an arena. Thus, it seems likely that the correlation between the percentage of dark satellites and of dark independent males is at least partly caused by migration between arenas.

Another explanation for this correlation is the possibility of changes of status of males with untypical plumages. The only case of a (temporary) change of status has been presented in the previous section (Va). This case referred to a "dark" satellite male on an arena with mainly "light" males. In the new role this male belonged to a "common" plumage group. This satellite was not inclined to migrate, on the contrary, he spent about 35% of his time on one arena (see above). It is thus possible that certain individuals of the "rare" plumage group instead of migrating possess a tendency to change their status, such that they become members of the "common" group.

TABLE 18

Relation between plumage colour of satellite males and duration of staying on the arena

	Mean percentages of time that *individual* satellite males were present on the arena:	
season and time spent in observation	Satellite plumage	Untypical plumage
1968 (97 hours)	10% (common) n = 9	8% (rare) n = 6 correction: 2% n = 5
1971 (22 hours)	4% (rare) n = 2	20% (common) n = 6

TABLE 19

Relation between plumage colour of resident males and attacking rate

Season:	Mean number of cases (per hour, per individual) that a resident male attacked another resident male: Independent plumages	attacked another resident male: Untypical plumages	was attacked by another resident male: Independent plumages	was attacked by another resident male: Untypical plumages
1968	0.62 (rare)	0.31 (common)	0.30 (rare)	0.45 (common)
1971	0.85 (common)	0.63 (rare)	0.62 (common)	1.43 (rare)

Migration and changes of status might be a consequence of a repulsion of males of "rare" plumage groups. To test this hypothesis I calculated for the earlier mentioned seasons (1968, 1971) the mean number of cases (per hour) that a resident male of either plumage group attacked another resident male, or was attacked by another resident male. Table 19 shows that in both seasons males with independent plumages attack more often, and are attacked less, than males with untypical plumages. There is no relation between being "common" and attacking, or between being "rare" and being attacked.

Another hypothesis suggests that males of "rare" plumage groups are not as successful in copulating as males of the "common" plumage groups, and for that reason stay for a relatively short period on the arena, or change their status. To test this possibility I calculated for the same seasons the mean number of resident copulations (per male, per hour). In both seasons individuals belonging to the "common" plumage group performed considerably more copulations than individuals of the "rare" group (Table 20). Thus, differences in copulation frequencies might play a role in the causation of the relation between the percentages of dark satellites and of dark independent males.

TABLE 20

Relation between plumage colour of resident males and copulation frequency

Season:	Mean number of copulations (per hour, per individual) by resident males with Independent plumages	Untypical plumages
1968	0.06 (rare)	0.16 (common)
1971	0.32 (common)	0.14 (rare)

c. Discussion.

In this chapter HOGAN-WARBURG's arguments for a genetical control of the behavioural differences between independent males and satellite males have been further examined. Her findings referring to constancy and early determination of the status of an individual (section Va) could not be confirmed unconditionally. Therefore it was necessary to discuss again how far the behavioural differences were genetically or environmentally controlled.

In many closely investigated species phenotypical diversity among individuals could be ascribed to genetical diversity (polymorphism; cfr. MAYR, 1963 and 1971). It is plausible that in the Ruff also, plumage diversity as well as behavioural diversity is controlled by genetical factors. On the other hand changes in the status of an individual, as observed, must be caused by environmental factors.

To explain this apparent contradiction one has to keep in mind that in the development of every behavioural trait both genotype and environment play a role (cfr. PARSONS, 1967; HINDE, 1970). A difference in behaviour between individuals can be ascribed to exclusively genetical factors if the individuals have been exposed to similar environmental conditions. It is self-evident that for dark and light coloured males on the same arena the environmental conditions are not similar. For instance light coloured resident males are attacked more often than dark coloured ones(Section Vb).

The status of males with independent plumages (any ruff and black head tufts) and males with satellite plumages (plain white ruff and head tufts, or plain white ruff and white head tufts with any pattern, or white ruff with any pattern and plain white head tufts) is supposed to be determined under most natural conditions (the status of a caged "satellite" male appeared to be modifiable (Section Va), in spite of his satellite plumage). The status of males with untypical plumages (intermediate colours) appeared, depending on the external situation, to be modifiable. The division into three plumage groups results in one intermediate and two extreme categories of males with respect to both behaviour and the plumage. It is likely that the individuals of each category are characterized by a distinct combination of genes. So, we may distinguish three kinds of mutually exclusive gene combinations. This suggest that we are dealing with two alternative homozygous groups of males (independent and satellite plumages) and one heterozygous group (untypical plumages). If this hypothesis is correct, and if the individuals of the distinct plumage groups do not strongly differ in fitness, one would expect that the numbers of individuals of the different plumage groups were in agreement with the Hardy-Weinberg law ($p^2 : 2pq : q^2$). Table 21 shows that HOGAN-WARBURG's data (p. 162), which include marginal males, do not give reasons to reject the hypothesis ($X^2 = 1.66$, df = 6, $p > 0.95$).

TABLE 21

Numbers of individuals of different plumage groups in different localities

plumage group:	Independent		Untypical		Satellite	
hypothetical genotype:	II		IS		SS	
locality:						
Schier.	11	(11.3)	16	(15.4)	5	(5.3)
Roder.	9	(9.5)	21	(20.0)	10	(10.5)
Hasselt	29	(26.9)	36	(34.2)	10	(10.9)
O.P.	30	(27.9)	29	(32.8)	11	(9.3)

$X^2 = 1.66$, df = 6, $p > 0.95$; (expected values in brackets).

$$\text{expected II} = \frac{(\text{II} + \frac{1}{2}\text{IS})^2}{\text{II} + \text{IS} + \text{SS}}$$

$$\text{expected IS} = \frac{2\ (\text{II} + \frac{1}{2}\text{IS})\ (\text{SS} + \frac{1}{2}\text{IS})}{\text{II} + \text{IS} + \text{SS}}$$

$$\text{expected SS} = \frac{(\text{SS} + \frac{1}{2}\text{IS})^2}{\text{II} + \text{IS} + \text{SS}}$$

(Adapted from HOGAN-WARBURG's data, p. 162).

An important implication of the hypothesis formulated above is that both the behaviour and some aspects of the plumage are controlled by the same set of genes (pleiotropy). It is likely that these genes indirectly influence the behaviour (indirect pleiotropy), since at least the behaviour of males with untypical plumages depends on the relation between own plumage and other plumages on the arena.

An alternative possibility (proposed by HOGAN-WARBURG, p. 213, 214), "in which two separate sets of genes, one controlling behaviour and the other controlling the plumage, are linked", can be rejected. If this is the case, one should also expect (by crossing over) the occurrence of satellites with independent plumages and independent males with satellite plumages, unless these gene combinations were lethal.

VI. THE EFFECTS OF BEHAVIOURAL DIMORPHISM ON MATING SUCCESS

Three possibilities in which satellite males might enlarge the copulation frequency of resident males can be distinguished:

(a) satellite males might contribute to the attraction of females,
(b) they might enlarge the duration of the visits of females, and

TABLE 22

Relation between presence of satellite males and presence of females on the arena (*number of samples in different situations*)

	satellites absent	satellites present
females absent	940 (817)	692 (815)
females present	156 (279)	402 (279)

$X^2 = 153$, df = 1, $p < 0.01$; (expected values in brackets).

(c) they might promote the crouching of females.
The influence of satellite males on these different aspects is investigated in the following sections.

a. Attraction of females.

1. *Correlations between visits of females and satellites.*

The presence of females and satellite males on an *arena* has been examined by means of a large number of samples, taken with intervals of one minute during 12 observation periods with durations of about 3 hours. The results obtained in one season on one arena are given in Table 22. It is shown that females and satellites are significantly more often simultaneously present than would be expected, if the visits of both categories occurred independently of each other ($X^2 = 153$, $p < 0.01$). The same phenomenon has been observed in other seasons and on other arenas. Furthermore for both females and satellites the mean number of individuals present is high during the presence of both categories, compared with the situation of only one category present (Table 23).

In the same way it can be shown that females and satellite males are relatively often simultaneously present on the same *residence* (Table 24; $X^2 = 418$, $p < 0.01$).

One might explain the high probability of females and satellites being

TABLE 23

Mean number of satellite males and females present on the arena *in different situations*

	mean number of satellites	mean number of females	number of samples
only satellites present	1.37		692
satellites and females present	2.00	1.63	402
only females present		1.33	156

TABLE 24

Relation between presence of satellite males and presence of females on residences (*number of samples in different situations*)

	satellites absent	satellites present
females absent	6052 (5896)	677 (833)
females present	357 (513)	228 (72)

$X^2 = 418$, df = 1, $p < 0.01$; (expected values in brackets).

simultaneously present by assuming that both categories arrive and depart relatively often together. This possibility has been checked.

For this purpose two events on an *arena* were considered to be simultaneous when they occurred within the same minute (intervals smaller than one minute could not be analysed in these data). If females and satellites arrive or depart independently of each other, the number of individuals of one category, arriving or departing simultaneously with the other category equals:
[(total number of arriving or departing individuals of one category) × (number of minutes with arriving or departing individuals of the other
On an *arena* the observed number of females and satellites arriving or
category)] / (total number of minutes observation time).
departing simultaneously with the other category was considerably higher than the values calculated with the preceding formula (Table 25; all cases $p < 0.01$).

On a *residence* simultaneousness of the arrival of a female and a satellite male has been analysed in a different way. Out of 10 cases of one female

TABLE 25

Number of satellite males and females arriving on or departing from the arena *simultaneously* (*within the same minute*) *with and without the other category* (*females and satellites*)

	with other category		without other category		X^2	probability
			Arrivals			
satellites	82	(20)	282	(344)	203	< 0.01
females	67	(20)	97	(144)	125	< 0.01
			Departures			
satellites	114	(13)	212	(313)	818	< 0.01
females	91	(13)	52	(130)	505	< 0.01

Expected values (calculation see text) are given in brackets.

and one satellite moving simultaneously on the arena, both individuals arrived 6 times on the same residence. In order to examine the significance of this result I watched the number of arrivals on the different residences during the presence of only one female or satellite which was moving on the arena. With these data I was able to calculate how often a female and a satellite would arrive on the same residence, when moving independently of each other during the same time period. The probability that one female and one satellite male arrive together on *one particular residence* is then equal to:

[(the number of arrivals of females on this residence) × (the number of arrivals of satellites on this residence)] / [(the total numbers of arrivals of females on residences) × (the total number of arrivals of satellites on residences)].

Thus, the probability that one female and one satellite male arrive simultaneously on *one of the residences* on the arena is equal to the sum of the values (calculated with the preceding formula) for all residences. The expected value for the earlier mentioned 10 cases (10 times the probability of one case) was equal to 1.27. The observed value (6) was significantly higher (Poisson distribution, $p = 0.002$).

2. *Causation of the correlations.*

The data of the previous section may be interpreted in at least three ways:

(i) satellites attract females,

(ii) females attract satellites, and

(iii) other factors attract both females and satellites.

In order to examine these possibilities, arrival on and departure from the *arena* have been further analysed. Table 26 shows that females depart more often together with satellite males or females, than that they arrive with them (a, b), or that satellites depart with them (c, d) (X^2, all cases $p < 0.05$). No difference in the group composition could be observed between arrival of satellites and arrival of females (e, f), or between arrival and departure of satellites (g, h). Table 27 shows to what extent satellite males and females were present on the arena before the arrival and after the departure of groups, composed of either one or more females, or one or more satellites and sometimes additional independent males. Satellite males were relatively more often present after the departure of female groups than before the arrival of female groups (a), or after the departure of satellite groups (b). Females were more often present before the arrival of female groups than before the arrival of satellite groups (c) (X^2, all cases $p < 0.05$). If females and satellites arrive or depart independently of the presence of other females or satellites on the *arena,* the proportions of cases with females or satellites present before arrivals and after departures should not be larger than the proportions of time that females or satellites were present on the arena during the same observations. Compared with these last proportions, satellite groups arrive and depart relatively often when there are no females present on the arena (d, e), and female groups depart relatively often when satellites are present on the arena (f) (Table 27: expected values; X^2, all cases $p < 0.05$).

TABLE 26

Number of satellite males and females arriving on or departing from the arena *together (in the same group) with and without satellite males or females*

		number of satellites		number of females
arriving	with satellites	88	e	54
	without satellites	159		104
		g		↑ a ↓
departing	with satellites	94	← c →	83
	without satellites	149		78
arriving	with females	74	f	59
	without females	173		99
		h		↑ b ↓
departing	with females	88	← d →	85
	without females	155		76

←——→ significant difference (X^2, $p< 0.05$).

These data on arrivals of females and satellites on an *arena* show that: (i) the presence of females and/or satellites is not correlated with the number of arriving female groups, and (ii) the presence of females is negatively correlated with the number of arriving satellite groups. The last result seems to be contradictory to the data of the previous section, where it was shown that females and satellites tend to be simultaneously present. Both results can be true, however, when the individual visits of satellite males are shorter during the absence of females, than during their presence on the arena. This has been analysed in Table 28. Satellite males meeting only other satellites on an *arena,* or meeting no other satellites and no females, pay significantly shorter visits than satellite males meeting only females (Wilcoxon test, $p < 0.05$). (When individuals met both females and

TABLE 27

Presence of satellite males and of females on the arena *before arrival and after departure of satellite or female groups (explanation see text)*

		satellite groups number of				number of female groups		
arriving when	satellites present	(78.6)		69		40		(41.3)
	satellites absent	(75.5)		85		41		(39.7)
						↕ a		
departing when	satellites present	(68.4)		60	←b→	36	←f→	(26.0)
	satellites absent	(65.7)		74		15		(25.0)
arriving when	females present	(41.1)	←d→	22	←c→	21		(21.1)
	females absent	(114.0)		131		60		(59.9)
departing when	females present	(34.9)	←e→	12		9		(13.3)
	females absent	(99.2)		122		42		(37.7)

⟷ significant difference (X^2, $p< 0.05$).
The expected values (in brackets) are calculated from the time proportion between absence and presence of satellite males and of females on the same arena.
(The relations indicated by letters are discussed in the text).

satellites on the arena, the situation often became too complex to record the duration of their visits properly). The durations of the female visits do not show any relation with the presence of females or satellites.

The data on departures of females and satellites from an *arena* show

TABLE 28

Influence of the presence of satellite males and of females on the duration of visits of satellites and females to the arena

during the presence of independent males and in addition:	Number and mean duration (in minutes) of visits of: satellite males number	mean duration	females number	mean duration
only satellites	48	4.1	41	4.5
		↕		
only females	18	7.6	4	3.5
		↕		
no others	31	4.5	13	6.7

⟷ significant difference (Wilcoxon's test, $p< 0.05$).

that: (i) the departure of females is positively correlated with the departure of other females or satellites, and (ii) the departure of females does not prevent satellites from staying. Thus, females depart either when other females or satellites depart, or without association with others; satellite males, however, mostly depart on their own. The finding that females follow other departing individuals is of further consequence, because some of these individuals start for other arenas. This tendency enables females to easily find arenas which were still unknown to them.

Arrival of females and satellites on *residences* has also been further analysed. If, during the selection of a residence, females and satellites are not influenced by other females and satellites present on the residences, the probability of a visit to one particular residence may be considered to be constant. These probabilities have been measured for each of the residences in situations with either only one female present or only one satellite present on the arena. When females or satellites are present on a number of residences, the probability that one of these residences will be selected equals the sum of the probabilities for each of these residences. The expected number of cases that 24 females and 49 satellites, which were observed while moving alone on the arena, would select a residence with satellites or females on it, is equal to the sum of the probabilities for each of these selections. The results are given in Table 29. It is shown that females prefer residences with satellites (Poisson distribution, p = 0.08). For satellite males no preference could be observed. (No more data could be collected because of the complicated observation technique). This result means that resident males can enlarge the number of female visits on their *residences* by tolerating satellite males.

TABLE 29

Arrival of satellite males and females on residences

	number of movements of a single:					
towards a residence	satellite male			female		
with satellite(s)	6	(6.83)	n.s.	7	(3.72)	p = 0.08
with 2 satellites	—	—		3	(0.58)	p = 0.02
without satellites	43	(42.17)	n.s.	17	(20.28)	n.s.
with female(s)	8	(9.48)	n.s.	2	(1.82)	n.s.
without females	41	(39.52)	n.s.	22	(22.18)	n.s.

For the calculation of the expected values (in brackets) see text. The probabilities are based upon a Poisson distribution.

b. Duration of female visits.

In the previous section it was shown that satellite males tend to stay for a shorter period on the arena, in the absence of females than during their presence. The duration of female visits to the arena was however not influenced by the presence of satellite males. In this section the extent to which females and satellites influence each other with respect to the duration of visits to *residences* will be analysed. The main part of these data were collected by Mrs G. van Rhijn-Baeyens.

The first step was a comparison between the durations of visits to residences by single females or satellites and by individuals of each category that were at least part of the time together on the residence with one

TABLE 30

Duration of visits of satellite males and females to residences *in relation to the presence of one individual of the other category (females and satellites)*

	number and mean duration (in minutes) of visits of:			
	satellite males		females	
	number	mean duration	number	mean duration
other category absent	89	4·1	77	4·7
other category present	25	7·0	25	7·4
arriving as first	8	11.4	11	11.7
arriving as second	12	3·8	9	2.9
arriving together	5	8.0	5	6.0
departing as first	7	3.0	8	3.1
departing as second	7	13.7	6	14.2
departing together	11	5·3	11	7.0

←→ significant difference (Wilcoxon's test, $p < 0.05$).

individual of the other category. For both females and satellites it could be shown that visits to residences with an individual of the other category had longer durations than visits without other individuals (Table 30, Wilcoxon's test, both cases $p < 0.05$). The second step, a more detailed analysis of these data, reveals that these correlations are caused by very long durations of visits of both females and satellites in situations where they were the first arriving and/or the last departing individual (Table 30). When the individual was the last arriving or the first departing one; no increase in the duration of visits could be observed.

These data cannot be explained by assuming that both females and satellites enlarge the duration of the visits of each other. In that case one would expect an effect in all categories of Table 30. However, at least two explanations remain:

(1) Individuals that stay for a long period on one residence meet with a relatively high probability individuals of the other category during that visit. The probability for 10 visits of one minute should be the same as for one visit of 10 minutes.

(2) Individuals that stay for a long period on one residence are very attractive for individuals of the other category (possible by their behaviour: *e.g.* crouching of females). The probability for 10 visits of one minute should be smaller than for one visit of 10 minutes.

In order to examine which of these two explanations is the most probable, I calculated, for short (< 10 minutes) and long visits (≧ 10 minutes) of females and satellites, the percentages of time spent together with individuals of the other category. Table 31 shows that this percentage does not depend on the durations of the visits. Thus the first explanation seems to be correct. These data do not give any support to the hypothesis that the presence of satellite males has the effect of increasing the duration of female visits to *residences.*

TABLE 31

Relation between duration of visits of satellite males and females to residences, *and the percentage of time spent together with the other category (females and satellites)*

Satellite visits:

	number	total duration (minutes)	minutes with other cat.	percentage
< 10 minutes	104	349	62	18
⩾ 10 minutes	10	194	34	18
Female visits:				
< 10 minutes	87	301	50	17
⩾ 10 minutes	15	249	46	18

c. Crouching of females.

Hogan-Warburg supposed that the presence of a satellite male on a *residence* has a positive influence on the copulation frequency of a resident male on a small arena; on a large arena, however, the copulation frequency would be negatively influenced (p. 184). The present data suggest neither a relation with arena size, nor a positive influence of satellites on the copulation frequency of resident males. Out of 445 copulations of resident males on arenas, varying in size from 3 to 28 resident males, only 13 copulations were performed while a satellite was present on the *residence.* Ten of these copulations occurred on a recently established arena; 8 of them took place on residences with many females. All 13 copulations with satellites on the residences were performed on medium sized arenas (6-8 resident males). Thus, copulations of resident males occurred very seldomly in situations with satellites on the residences, although normally about 30-60% of the females on residences are accompanied by satellite males.

In view of the attractiveness of satellites for females (section VIa) it is surprising that copulating resident males normally do not have satellite males on their residences. To throw some more light on this problem I studied the aggression of resident males towards satellites. Table 32 shows that attacks on satellites are relatively rare when there are no females on the arena; resident males with females on their residences, however, attack satellites very often ($X^2 = 15.1$, df $= 2$, $p < 0.01$). It could be shown

TABLE 32

Relation between the number of attacks of resident males on satellite males, and the presence of females

	number of attacks on:	
	satellite males	independent males, satellites present
no females on arena	9 (20)	147 (136)
females on arena	47 (46)	310 (311)
females on residence	24 (14)	88 (98)

$X^2 = 15.1$, df $= 2$, $p < 0.01$

	satellite males	independent males, satellites present
females on residence	24 (17)	88 (95)
females elsewhere	47 (54)	310 (303)

$X^2 = 5.2$, df $= 1$, $p < 0.05$, (expected values in brackets).

TABLE 33

Relation between the number of attacks of resident males on satellite males, and copulation frequency

number of copulations during periods of ten days	number of ten days periods	number of attacks on satellite males
5 and more	7	36 (23.7)
1-4	7	19 (23.7)
0	7	16 (23.7)

$X^2 = 9.8$, df = 2, $p < 0.01$; (expected values in brackets).
The available time is about constant during a ten days period.

that the number of attacks on satellites was higher in the situation with females on the residence than in the situation with females elsewhere on the arena (Table 32, $X^2 = 5.2$, df = 1, $p < 0.05$). Table 33 shows that resident males with high copulation frequencies attack satellite males more often than resident males with only a few copulations ($X^2 = 9.8$, df = 2, $p<0.01$). In Table 34 it is shown that resident males with a high copulation frequency attack satellites relatively often when they have no females on their residences; resident males with only a few copulations mostly attack satellites when there are females on their residences ($X^2 = 9.0$, $p < 0.01$). These data suggest that in unsuccessful resident males the rise in aggression is a short lasting reaction to the presence of females, while in successful resident males the increased readiness to attack is of longer duration.

The previous data do not show whether the aggressiveness of successful resident males is caused by copulations or the factors underlying them or whether the copulation success itself is positively influenced by a high level of aggressiveness. The next observation give some support to the first possibility. A resident male was once observed performing 14 copulations within two hours. During the week preceding this observation neither copu-

TABLE 34

Influence of the presence of females on the residence *and of the copulation frequency of the resident male on the number of attacks on satellite males*

number of attacks on satellite males by males with:	no females on residence	females on residence
5 or more copulations during a ten days period	30 (24)	6 (12)
4 or less copulations during a ten days period	17 (23)	18 (12)

$X^2 = 9.0$, df = 1, $p < 0.01$; (expected values in brackets).

lations, nor excessive aggression towards satellite males was seen. During the first copulations the level of aggression towards satellites did not seem to be changed, but the periods between the last copulations were almost exclusively spent in aggressive encounters with satellite males on different places on the arena.

The alternative hypothesis that the mating success of resident males is positively influenced by a relatively high level of aggressiveness towards satellite males cannot be rejected. Probably this hypothesis is also true in view of the fact that resident males are often unable to copulate when they fail in expelling satellites from their residences. Both effects together (increase of aggression after copulation and more copulations when the level of aggression is high) can be considered as a positive feed-back system.

TABLE 35

Percentage of females simultaneously present with satellite males on residences *in relation to the copulation frequency of the resident male*

number of copulations during periods of ten days	percentage of females together with satellites
5 and more	22
1-4	30
0	66

A possible consequence of the increase of aggression towards satellite males is shown in Table 35. In successful resident males the percentage of females simultaneously present with satellite males on their residences is lower than in unsuccessful resident males.

These data do not prove that satellite males have a negative influence on crouching of females. It only gives indirect evidence for the hypothesis that resident males no longer profit from satellite males when they have females on their residences. This phenomenon is probably caused by a high activity of resident males when they have satellites on their residences (cfr. Chapter IV). Evidence has been obtained by Miss R. L. de Boer that a high activity level is negatively correlated with crouching of females (Table 36; $X^2 = 5.6$, $p < 0.05$).

d. After effects of visits of females and satellites to *residences*.

The preference of females for residences with satellite males, and the tendency of resident males to attack satellites might have consequences over a long period. Both phenomena together might cause regular fluctuations in the number and in the durations of female and satellite visits to residences. When the extent of satellite visits is large and the extent of female visits is small, one would expect an increase of the extent of female visits. When the extent of both female and satellite visits is large, resulting in a large overlap of visits of both categories, one would expect a decrease in the extent of satellite visits.

This hypothesis has been further investigated. To this end I have compared the number and the durations of visits of females and of satellites to the various *residences* during continuous observation periods (1-4 hours), separated by intervals of ½-3, 4-8, and 9-14 days. Because of the tremendous fluctuations in the number and the durations of these visits, probably often caused by external circumstances, the following procedure has been chosen: for each *resident* male the sum of the durations of all visits of females and of satellite males during the observation period was expressed as a percentage of an expected value. This expectation was based upon the sum of the durations of all visits of females and satellites to the *arena* during the same observation period, divided by the total number of resident males present in that period (thus a random distribution of both female and satellite visits over all resident males). The percentage is a measure of the extent of the visits of females or satellites to a certain resident male during a certain observation period. A resident male was considered to obtain a small extent of visits when the value was smaller than 40%, a medium extent when it was 40% or larger but smaller than 120%, and a large extent when the observed value was 120% or larger of the expected one.

TABLE 36

Relation between the activity level of the resident male and crouching of females on his residence

number of activities of the resident male	number of cases: with crouching		without crouching	
$\geqslant$ 1 / minute	2	(5.8)	18	(14.2)
$<$ 1 / minute	9	(5.2)	9	(12.8)

$X^2 = 5.6$, df = 1, $p < 0.05$; (expected values in brackets).

First, I tried to find out whether for the same resident males, the distribution of small, medium, and large extents of the visits of the females or satellites was independent of (a) the distribution of the visits of the

TABLE 37

Probabilities (%) of independence between the extents of visits of satellite males and females to the same residence *during the same or different observation periods*

extents of visits (on day 0) of:	satellites		females	
compared with extents of visits of:	satellites	females	satellites	females
after interval (in days) of:				
0	= 0% (+)	< 1% (+)	< 1% (+)	= 0% (+)
½- 3	< ½% (+)	< 25% (+)	< 5% (+)	< 5% (+)
4- 8	> 75%	< ½% (+)	> 50%	< 10% (+)
9-14	< 10% (—)	< 25% (+)	< ½% (—)	< 50% (+)

(+) tend to a positive correlation. (—) tend to a negative correlation.

other category during the same observation period (interval = 0 days); and (b) the distributions of the visits of the same, and the other category during later observation periods (interval = ½-3, 4-8, and 9-14 days). It could be shown that in many cases different distributions were highly dependent on each other (Table 37).

Second, I examined whether the dependent distributions tended to be positively (+) or negatively (—) correlated (Table 37). The data suggest that the extent of both female and satellite visits remain positively correlated with the extent of female visits during later observations periods, even with intervals of 9-14 days. The extent of both females and satellite visits tends to be positively correlated with the extent of satellite visits until at least 3 days later. When the interval becomes longer than about 8 days, however, the correlation becomes negative.

Third, I have calculated the means of the extents of the visits of both females and satellites simultaneously with, and following small and large extents of visits of females as well as satellites (simultaneously: interval = 0 days; following: interval = ½-3, 4-8, and 9-14 days; small extents: < 40%; large extents ≧ 120%; see Figure 11). It is shown that after an interval of 9-14 days: (i) a large extent of female visits results in a large extent of female visits and a small extent of satellite visits; (ii) a small extent of female visits results in a relatively small extent of female visits and a large extent of satellite visits; (iii) a large extent of satellite visits results in a relatively small extent of satellite visits and a large extent of female visits; and (iv) a small extent of satellite visits results in medium extents of both satellite and female visits.

The positive correlation between the extents of female visits on days

TABLE 38

Differences in the proportions of satellite and female visits between 5 resident *males*

male	satellite visits				female visits			
number	mean	min	max	diff	mean	min	max	diff
1	13.2 %	9 %	28 %	25 %	19.5 %	9 %	31 %	22 %
2	12.8 %	3 %	28 %	25 %	8.9 %	2 %	19 %	17 %
3	13.6 %	2 %	25 %	23 %	9.0 %	2 %	0 %	17 %
4	20.9 %	2 %	43 %	41 %	9.4 %	0 %	23 %	23 %
5	22.5 %	4 %	45 %	41 %	3.5 %	2 %	5 %	3 %

mean = mean of the values of all 5 days periods, min. = minimum value (lowest value of the 5 days periods), max. = maximum value (highest value of the 5 days periods), diff. = difference between max and min (see also text).

◄——► significant difference (Wilcoxon's test, $p < 0.05$).

separated by long intervals can be easily explained. This correlation is likely to be caused by large differences in the extents of female visits between individual resident-males, and small variations within individuals. A comparison between 5 resident males which were present on the arena for at least 20 successive days, affirms this suggestion (Table 38). For each of these *resident* males the sum of the durations of all female and satellite visits observed during periods of 5 days, was expressed as a percentage of the sum of the durations of all visits to the *arena* during the same period. No differences could be observed

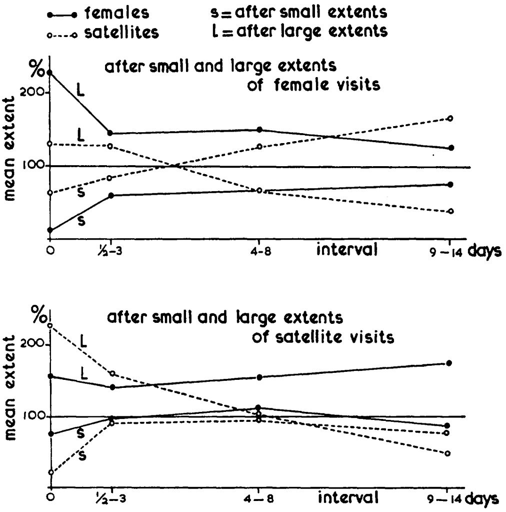

Fig. 11. Influence of small (< 40%) and large (⩾ 120%) extents of visits of females and satellites on the mean extents of later visits of both categories to the same resident males.

between the 5 individuals in the proportions of satellite visits (Wilcoxon's test). The proportions of female visits, however, differed clearly between some of the males. One male was visited significantly more often by females than the other four, another male received a significantly smaller proportion of female visits than three males. For each individual the difference between the highest and the lowest proportion of satellite visits was always higher than that of female visits (Sign test: $p < 0.05$; Wilcoxon's test: $p < 0.02$).

The finding that a large extent of satellite visits results, after 9-14 days, in a small extent of satellite visits, demonstrates that the extent of satellite visits undergoes large oscillations. One would then expect the extent of female visits to oscillate in about the same direction, due to the extents of female and satellite visits during the same observation period being positively correlated with each other. The similarities in these oscillations have been checked with the data of the 5 day-periods. Out of 39 transitions of the proportions of visits of females and satellites to individual *resident males*, 27 cases have been observed with changes in the same direction (either an increase or a decrease of both proportions); in 8 cases the directions were opposite; in 4 cases one of the proportions did not change. This result is highly significant (Sign test: $p < 0.01$). The finding that the extent of female visits and, the extent of satellite visits 9-14 days later, are negatively correlated with each other also demonstrates the large oscillations in the extents of the visits. One might also expect a negative correlation in the reversed situation, *i.e.* between the extent of satellite visits and the extent of female visits 9-14 days later, because of the positive correlation between the extents of female and satellite visits during the same observation period. This negative correlation could not be affirmed. On the contrary, a large extent of satellite visits resulted in a large extent of female visits after 9-14 days (a small extent of satellite visits resulted in a medium extent of female visits). This result supports the hypothesis formulated in the beginning of this section, namely that resident males will lower the extent of satellite visits, when the extents of both female and satellite visits are high. The intolerant behaviour of resident males apparently does not strongly influence the extent of female visits.

e. Further investigation of the factors influencing female and satellite visits.

In the previous sections it is shown that the visits of females and satellites are highly dependent on each other. We will now examine the importance of this mutual dependence in relation to other factors influencing number and durations of visits to *residences*.

One might expect that female and satellite visits are determined by the circumstances on the residence during those visits (direct stimuli) and by experience on that residence during previous visits (conditioning). Satellite males normally maintain their individual preferences for residences over a long period (several weeks). Table 39 shows a comparison between the visiting rates of one individual satellite male and the sum of the visiting rates of the other satellites for 9 resident males during 6 periods of 10 days. These visiting rates are expressed as a percentage of the sum of the durations of all observed visits to *all* residences during that period. Since a high visiting rate was connected with copulation of satellites (the one individual performed 10 copulations — out of 12 — on the residence of male number 5), it is likely that experience is an important factor. A few females could be individually recognised during a few days; some of them seemed to have preferences different from the mean preference of other females. Although no quantitative evidence could be obtained, it is likely that in females conditioning also plays a role in the selection of a residence.

TABLE 39

Visiting rates (see text) of one individual satellite (first columns) and the sum of the visiting rates of the other satellites (second columns) for 9 resident males during 6 periods of ten days

resident males:

period	1		2		3		4		5		6		7		8		9	
A	7	18	2	8	12	8	13	20	46	26	0	0						
B	0	9	17	15	26	10	0	7	48	34	7	9						
C	7	13	4	6	16	5	11	47	59	24	3	5						
D	32	15	6	4	9	6	14	11	16	9	7	35						
E	0	1	3	1	13	7			53	16	0	26	30	7	0	36	0	0
F	0	17	37	38	0	0			1	3					0	0	62	62

Immediate preferences of females for certain resident males (independently of the role of conditioning) depend on the behaviour of these resident males, and on the presence of other females and satellites on their residences. The influence of the behaviour of the resident male has been studied by Miss R. L. de Boer. She demonstrated that a resident male can enlarge the number of female visits by (i) performing a high rate of "turning" displays on his residence, and (ii) starting off with "sequences" of movements (after periods of immobility) in which all resident males then participate (Table 40, X^2, both cases $p < 0.05$). She further showed (Table 41) that these aspects of the behaviour remained more or less constant during successive periods for each of the resident males, and were

TABLE 40

Influence of "turning" displays, and of starting off with "sequences" on selection of resident *males by females*

behaviour of the resident male before the choice of the female:	number of cases: female goes to the residence	female does not go to the residence
"turning"	30	20
	(25)	(25)
no "turning"	4	14
	(9)	(9)

$X^2 = 6.1$, df $= 1$, $p < 0.05$.

	female goes to the residence	female does not go to the residence
starting off	26	14
	(20)	(20)
no starting off	8	20
	(14)	(14)

$X^2 = 7.3$, df $= 1$, $p < 0.05$; (expected values in brackets).

also correlated with female visits in this comparison. Thus a number of resident males seem to have better tactics for attracting females than others.

The influence of the presence of other females follows from the fact that females often move in a group on the arena. The choice of a residence by one female apparently determines the choice of the other members of the group. Only 4 cases of 2 females moving simultaneously on the arena have been analysed. Both females arrived on the same residence in all cases. An expected value (0.62) was calculated in the same way as for one female and one satellite (Section VIa 1). The observed value was significantly higher (Poisson distribution, $p = 0.003$).

TABLE 41

Mean frequency (number/minute) of turning displays, and starting off with sequences shown by 5 resident males during the presence of females on the arena in two successive periods (= 30/4-3/5, and B = 4/5-12/5 1971)

	turning		starting off		female visits	
	A	B	A	B	A	B
males						
1	1.7	1.5	0.6	0.6	28	11
2	1.4	1.6	0.5	0.2	8	2
3	0.0	0.8	0.1	0.2	1	2
4	1.5	1.2	0.4	0.3	27	1
5	0.5	0.5	0.3	0.3	4	1

female visits = sum of durations in minutes of all visits per 100 minutes.

Immediate preferences of satellites for certain resident males also depend on the behaviour of these resident males, and on the presence of females. The importance of the behaviour of the resident male has been discussed already in Section VIc. It was demonstrated that this behaviour could be either tolerant or intolerant, depending on the presence of females (a short lasting reaction), and on the copulation frequency (a reaction of longer duration). The direct influence of the presence of females on the selection of a residence by satellites has been affirmed by Mrs G. van Rhijn-Baeyens. Out of 10 cases of one female and one satellite arriving on the same residence within a few seconds, 9 cases have been observed in which the satellite male followed the female towards the residence (Sign test, $p < 0.05$). Thus it is obvious that females can determine the choice of satellite males in certain circumstances.

f. Discussion.

In this chapter the influence of satellite males on the copulation success of resident males has been analysed. We will now discuss to what extent a co-operation with satellites contributes to the fitness of resident males. For this purpose it is necessary to know which factors determine the copulation frequency of a resident male, when the copulation frequency is assumed to be a suitable measure for fitness.

The success of a resident male depends on the density of visits of females to his residence, in the absence of satellites. This density of "free female" visits is positively influenced by the density of female visits and negatively by the density of satellite visits. (The "density" is the sum of the durations in minutes of all visits during one day). Thus a high copulation frequency might be expected when the density of female visits is high, and the density of satellite visits is low. Nevertheless, resident males are unable to maintain such a situation, because the density of female visits is largely determined by the density of satellite visits (high densities of female visits are seldomly combined with low densities of satellite visits — cfr. Section VIa and d). Thus resident males cannot obtain high densities of female visits without tolerant behaviour towards satellites, hence high copulation frequencies can only be reached when the density of satellite visits is controlled in an adaptive way.

In order to throw some more light on this problem, day to day alterations in the copulation frequency of a resident male have been studied by means of a mathematical model, based on data presented in this chapter. The main underlying assumption is the direct relation between copulation frequency and density of "free female" visits (FF). This density is equal to the density of female visits minus the density of visits of females simultaneously present with satellite males, and can be calculated with formula (1):

$$FF = F - (F \times S) / A \qquad (1)$$

F is the density of females visits, S the density of satellite visits. If females and satellites visit residences independently of each other, parameter. A should be equal to the duration — in minutes — of the daily period that females and satellites can visit residences (about 600 minutes). It has been shown previously that females and satellites are much more often present on the same residence: in table 24 the observed value is about 3 × the expected one. Thus an approximation of parameter A is: 600 / 3 = 200 (minutes).

It is obvious that alterations in the copulation frequency are due to changes in the densities of both female and satellite visits. The density of female visits depends on experience of females, behaviour of the resident male, and on the presence of other females and satellites (Section VIe). For the sake of simplicity it was assumed that each time a residence was selected by a female this was caused by only one of these factors. Thus some female visits were only influenced by experience, others were directly attracted by the resident male, *etcetera*. The density of visits of females attracted by other females depends on the density of visits of females already caused by the other factors. Hence, the density of female visits is equal to the sum of the effects of experience, presence of satellites, and direct attraction, multiplied by a value referring to the effect of the presence of other females (formula (2)).

$$F = [(B \times F') + (C \times S) + D] \times E \qquad (2)$$

The expression (B × F′) corresponds to the proportion of returning experienced females (F′ is the density of female visits on the previous day); (C × S) is the proportion of females attracted by satellites; D is the proportion of females attracted directly by the resident male; E refers to the effect of attraction by other females. The parameters B, C, D, and E will be further explained below.

The density of satellite visits depends on experience of satellites, behaviour of the resident male, and on the presence of females (Section VIe). This could also be approximated with formula (3):

$$S = (G \times S') + (H \times F) + I \qquad (3)$$

The expression (G × S′) corresponds to the proportion of returning experienced satellites (S′ is the density of satellite visits on the previous day); (H × F) is the proportion of satellites attracted by females; I is the proportion of satellites attracted directly by the resident male.

Thus the density of "free female" visits, and the copulation frequency, depends on the densities of both female and satellite visits; these densities are linked up with: (i) each other, (ii) the densities on the previous day, and (iii) the values of the different parameters (B, C, D, E, G, H, and I). We will now examine for one average abstract resident male, which values correspond with those parameters. It is self-evident that these values are influenced by the supply of females and satellites on the arena. The effect of this supply, however, is comparable in all resident males. It would be too difficult to incorporate variations of such factors in the model, hence they were assumed to remain constant. Differences in the values of a parameter within or between resident males are caused by factors directly concerning the individuals. Because the behaviour of resident males towards females remains constant within an individual (Section VIe), it is likely that the values of B and D also remain constant. The values of C and E are supposed to remain constant too, since the presence of satellites and other females can be regarded as constant stimuli for females. The behaviour of resident males towards satellites is not constant (tolerant — intolerant), thus it is probable that G and I can adopt different values within an individual. Also the effect of the presence of females on satellites (parameter H) does not remain constant, because even during the presence of females, ultimately the behaviour of the resident male determines whether a satellite can enter the residence, or not. For the sake of simplicity it has been assumed that G, H, and I can adopt only two values within an individual (tolerant — intolerant). Since the transition from tolerant to intolerant behaviour occurs very rapidly (Section VIc), this simplification can be regarded as a fair approximation.

Quantitative approximations of the different parameters (formula 2, formula 3 during tolerance, and during intolerance) for one average abstract resident male could be calculated roughly by applying these formulas to *observed* densities of female and satellite visits. Since many unknown values were involved, only those observations have been selected in which the effects of some of the parameters (*e.g.* experience on the previous day) could be neglected (*e.g.* because there were no females or satellites present on the residence on that previous day), or could be calculated on account of findings from other observations (*e.g.* half of the females normally return on the next day to the same residence). Using this method the next values were obtained:
$B = 0.5$, $C = 0.4$, $D = 2$, $E = 1.25$;
during tolerance:
$G = 1.2$, $H = 0.4$, $I = 5$;
during intolerance:
$G = 0.4$, $H = 0.2$, $I = 1$.

Tolerant behaviour of a resident male changes into intolerant behaviour when either the density of female visits, or the copulation frequency, or both become high. Tolerant behaviour reappears both when the density of female visits is low again, and when the copulation frequency is low for at least some days (the increased readiness to attack is of longer duration, cfr. Section VIc). These findings suggest that the tolerant — intolerant transition is controlled by two threshold values (density of female visits, and copulation frequency), and by a latency (after effect of copulations). Although no data are available, it is assumed that these parameters are more or less constant within an individual.

The threshold values and the duration of the latency have been determined for the average abstract resident male. Densities of female visits above 60 (minutes/day) are mostly accompanied by intolerant behaviour towards satellite males; copulation frequencies above 6 (per day), which (for an average abstract male) is equivalent to a density of 30 (minutes/day) "free female" visits, have about the same effect, but in this case however, the intolerant behaviour is maintained for about 5 days (latency) after a drop below this value.

It is now possible to use the model to stimulate the fluctuations in (a) the densities of both female and satellite visits, and (b) the copulation frequencies (densities of "free female" visits). The values of the different parameters have been substituted in the formulas:

(1) $FF = F - (F \times S) / 200$

(2) $F = [(0.5 \times F') + (0.4 \times S) + 2] \times 1.25$

(3) $S = (1.2 \times S') + (0.4 \times F) + 5$ (tolerant resident male)

$S = (0.4 \times S') + (0.2 \times F) + 1$ (intolerant resident male)

Using the formulas, the threshold values, and the duration of the latency, I have calculated the fluctuations in the densities of female, satellite, and "free female" visits over a period of 25 days, starting with densities of zero (Figure 12). These fluctuations are in agreement with the data presented in Section VIa (Tables 37 and 38, Figure 11).

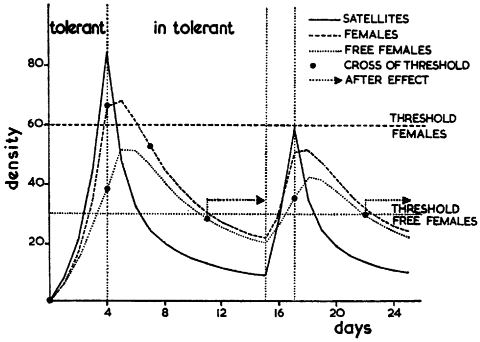

Fig. 12. Simulation of fluctuations of the densities of female, satellite, and "free female" visits to the same resident male (control).

The influence of the different parameters on the average copulation frequency of a resident male has been studied by means of simulations in which each time only one parameter value of the first simulation (control = Figure 12) has been changed (Table 42). For each of the parameters a smaller and a larger value has been substituted. From a comparison between the control, the smaller, and the larger value it can be concluded that a resident male obtains a high density of "free female" visits, thus a high number of copulations, if:

TABLE 42

Means of the densities of satellite visits, female visits, and "free female" visits

		Sat	Fem	Free Fem
first simulation (control)		23.86	36.89	30.57
	B = 0.4	28.79	31.36	23.72
	B = 0.6	28.33	60.77	49.61
(females)	C = 0.3	29.86	35.12	27.35
	C = 0.5	17.75	34.49	30.11
	D = 1	22.97	31.18	25.52
	D = 5	18.07	38.48	33.45
	G = 0.8	29.15	29.58	25.06
	G = 1.5	21.38	33.78	28.56
(tolerant satellites)	H = 0.3	20.24	31.72	26.98
	H = 0.5	21.82	33.60	28.15
	I = 2	22.69	35.31	29.35
	I = 10	24.46	37.69	31.19
	G = 0.3	21.63	32.58	26.75
	G = 0.5	30.67	44.15	34.38
(intolerant satellites)	H = 0.1	21.61	34.43	28.52
	H = 0.3	28.93	42.41	34.00
	I = 0	21.91	34.11	28.41
	I = 3	24.53	37.48	31.01
latency after a high success	= 2	24.16	36.66	30.24
	= 10	22.23	33.80	27.56
threshold female visits	= 40	23.86	36.89	30.57
	= 80	23.86	36.89	30.57
threshold "free female" visits	= 20	13.30	23.20	20.79
	= 40	33.24	48.98	37.27

Every time only one of the values of the different parameters of the fist simulation (= control, Fig. 12) has been changed. A smaller and a larger value have been substituted for each of the parameters.

(i) the parameters relating to the density of female visits are high (B, C, and D),

(ii) the parameters relating to the density of satellite visits during *intolerance* are relatively high (G, H, and I), and
(iii) the threshold value for copulations (or "free female" visits) is also high.

The number of copulations was not clearly influenced by a change of:
(iv) the parameters relating to the density of satellite visits during *tolerance* (G, H, and I),
(v) the threshold value for female visits, and
(vi) the latency after a high copulation success.

In order to understand the first conclusion (i) it is useful to examine to what extent a resident male is able to attract females without having satellite males. Formula (2) can be adapted to this situation:

$$(2') \qquad F = [(B \times F') + D] \times E$$
$$= (B \times E \times F') + (D \times E)$$

If $(B \times E) < 1$ (which happens to be true for all or almost all resident males) F will approximate a limit value after a number of days (thus $F \approx F'$). This limit can be calculated for different values of B, D, and E:

$$F = (B \times E \times F) + (D \times E)$$
or $$F\,[1 - (B \times E)\,] = D \times E$$
or $$F = (D \times E) / [1 - (B \times E)]$$

For the values of B and D in Table 42, F will approximate:

Control : 2.5 / 0.375 = 6.67
B = 0.4 : 2.5 / 0.5 = 5.00
B = 0.6 : 2.5 / 0.25 = 10.00
D = 1 : 1.25 / 0.375 = 3·33
D = 5 : 6.25 / 0.375 = 16.67

Thus the densities of "free female" visits (in these cases equal to the densities of female visits) and the copulation frequencies do not reach high values, if a resident male does not co-operate with satellites.

High densities of satellite visits can easily be acquired by a resident male if he behaves tolerantly. It has been shown already that the density of female visits increases when satellites pay many visits to the residence. A disadvantage of high densities of satellite visits is a low density of "free female" visits; if $S \geqq A$ (formula (1)) the density of "free female" visits is even equal to zero (in fact negative):

$$FF = F - (F \times S) / A$$
$$= F\,(1 - S / A)$$

Thus if a resident male remains tolerant towards satellite males, the copulation frequency drops to zero.

Intolerant behaviour can be started after high copulation frequencies or after high densities of female visits. Figure 12 showed the effect of the threshold for "free female" visits (copulations). The effect of the threshold for female visits becomes clear if the threshold value for copulations is high (Figure 13). In Table 42 (with a relatively low threshold value for copulations) no effect could be observed after a change in the value of the threshold for female visits. Thus, the fifth conclusion (v) must be changed: a high threshold value for female visits can bring on a high copulation frequency if the threshold value for "free female" visits is also high. The second conclusion (ii) also requires further explanation.

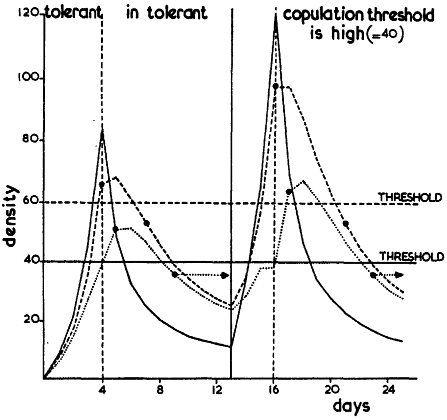

Fig. 13. Simulation with a high threshold for density of "free female" visits (copulation threshold).

Resident males with low values for G, H, and I during intolerance (thus highly intolerant behaviour) are able to lower rapidly the density of satellite visits. Owing to this the densities of female visits, and the copulation frequencies drop below the threshold values within a few days. The mean copulation frequency depends on the proportion of time with high densities of "free female" visits (above threshold). This proportion is relatively high in males with relatively high values for G, H, or I during intolerance (thus fairly intolerant behaviour). Such differences in the degree of intolerance are shown in Figure 14.

In summary then, a co-operation with satellite males is very adaptive for most resident males, if tolerant and intolerant behaviour alternate regularly. The "success" of a resident male strongly depends on the heights of the threshold values (for female visits and copulations), and in addition on the degree of *intolerance*. Nevertheless the degree of *tolerance* does not have a distinct influence on the copulation frequency. Exceptional resident males, which are able to enlarge the density of female visits without admitting satellites on their residences (thus (B × E) $\geqq$ 1 in formula (2)), do not profit by penetrating satellites.

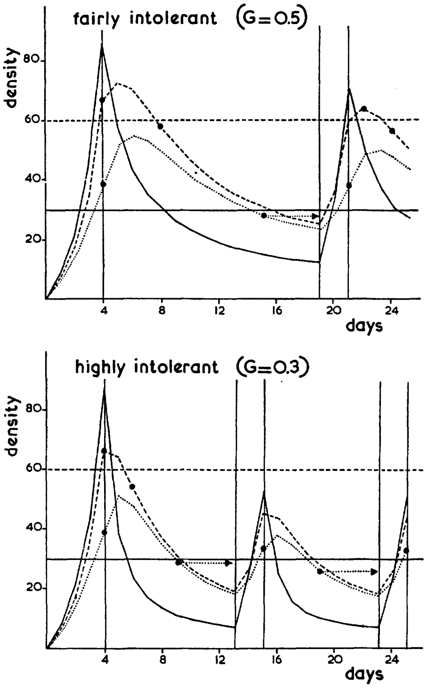

Fig. 14. Simulation of a highly intolerant and of a fairly intolerant resident male.

VII. SURVIVAL OF BOTH BEHAVIOURAL TYPES IN A POPULATION

a. Introduction.

When the differences in status between independent males and satellites at least partly reflect differences in genotype (Chapter V), we are dealing with a genetical polymorphism. This has been defined by Ford (1940, 1945, 1964) as "the occurrence together in the same locality of two or more discontinuous forms of a species in such proportions that the rarest of them cannot be maintained by recurrent mutation".

It is likely that this kind of polymorphism is a widespread phenomenon in the Ruff (*the Netherlands*: Selous, 1906-1907; Hogan-Warburg, 1966; *Denmark*: BANCKE & MEESENBURG, 1952, 1958; *Sweden*: Julia WENTWORTH, pers. comm.; *U.S.S.R.*: L. N. DOBRINSKY, pers. comm.).

Two basic types of genetical polymorphism can be distinguished: balanced and transient. In the case of the Ruff transient polymorphism is not very likely, since both phenotypical groups have existed for at least 65 years (SELOUS). Thus, it is probable that we are dealing with a balanced polymorphism (in the sense of FORD), "being maintained by contending advantages and disadvantages at a level determined by the relative strength of the opposing selective forces to which they are subject" (FORD, 1964).

Maintenance of genetical diversity in a polymorphic species or population can be a consequence of superiority of heterozygotes (balanced polymorphism *sensu stricto*; MAYR, 1963, 1970) or the diversity of the local environment in space and time (ecological protection). The last possibility may imply that different phenotypes utilize different subniches. In the next sections I want to discuss to what extent these possibilities are applicable to the Ruff.

b. Superiority of heterozygotes.

Some of the genetic variation in populations is directly maintained by natural selection. Two alleles can be maintained in a population at high frequencies if the fitness of the heterozygotes is higher than that of either homozygote, even if one of these homozygotes is lethal.

If status in the Ruff is controlled by only one gene or supergene (cfr. FORD, 1964), the genotype distribution in the two phenotypical groups could be realised in three different ways:

i. one of the homozygotes is lethal; one of the phenotypical groups contains homozygotes, the other one contains heterozygotes;
ii. one of the alleles is dominant; one of the phenotypical groups contains homozygotes and heterozygotes, the other one contains only homozygotes; and
iii. the kind of phenotype of a heterozygous individual is controlled by environmental factors; each phenotypical group contains homozygotes and heterozygotes.

The inconstancy of the status of males with untypical plumage colours (Chapter V) is compatible with this last possibility, and incompatible with the first and the second one.

One might assume that individuals belonging to this untypical plumage group represent the heterozygous condition. It has been supposed that these individuals were able to adapt their status to environmental circumstances (Chapter V); under this condition it is possible that they have a higher fitness than individuals belonging to the independent and satellite plumage group (constant status). Thus superiority of heterozygotes might play a role in the maintenance of behavioural polymorphism in the Ruff.

c. Differential niche utilization.

The diversity of the local environment can also maintain polymorphism in a population. "The contribution to fitness made by a given phenotype changes in time and space and this causes changes in the selective value of genes. A gene that is inferior under some conditions is superior under others and the chance that it will be preserved in the gene pool is thereby greatly increased" (MAYR, 1963).

LUDWIG (1950) calculated that a genotype utilizing a novel subniche could be maintained in a population even if its fitness was inferior in the normal niche. By means of mathematical models LEVENE (1953) and LI (1955) examined under what circumstances genetical heterogeneity can be maintained without superiority of heterozygotes. They concluded that in a random mating population one or more stable equilibria of genotype distributions could be obtained under differential local selection pressures (different niches). Their statements were based upon a random distribution of all individuals of a population over all subniches (no differential habitat selection by genotypes). Individuals remained in their subniche until the next reproductive period. It has been calculated by DEMPSTER (1955) that equilibria can only exist if in each subniche the number of individuals surviving until each next reproductive period is constant, and thus independent of the proportions of the different genotypes which were present in the population after the previous reproductive period. This implies that when well adapted genotypes are common in the original group of individuals in a subniche (after the previous reproductive period), the probability of survival of the individuals of all different genotypes in that subniche is lower than when well adapted genotypes are rare. Such a negative relation between fitness and relative frequency has been extensively studied in experimental populations of *Drosophila pseudoobscura* (EHRMAN *et al.*, 1965; EHRMAN, 1966). They supposed this phenomenon to be very common. A causal explanation has not been given.

In the Ruff we can discuss the diversity of the local environment only with respect to the arena system (Chapter VI). Independent males and satellite males play different roles in this system. The first phenotypical group is specialized in the establishment and maintenance of mating places; the other group in the attraction of females towards those mating places and towards arenas. Thus, each phenotypical group occupies its own subniche, moreover, both groups are highly dependent on each other. Independent males are not successful when they do not co-operate with satellites (Chapter VI) and satellites can seldomly stimulate females to crouch for them in the absence of resident males (mating places). This reasoning suggests that in the Ruff also the fitness of individuals of either phenotype is negatively correlated with their relative frequencies. A high frequency of the one phenotype results in a low number of descendents per individual belonging to that phenotype, because of a poor co-operation with the other phenotype.

We may thus assume that relative frequency and the copulation frequency are negatively correlated, if the number of descendants per individual is taken to be dependent on the number of copulations. My data do not show such a correlation, but this may be caused by the small fluctuations in the relative frequencies I observed. HOGAN-WARBURG (p. 215) presented some evidence for this correlation, although its value is somewhat doubtful. Her explanation (p. 216) for it was based upon the supposition that the relative copulation frequency of satellite males is negatively influenced by an increase of the number of resident males and/or of the number of satellites on the arena. Both on a large arena and on an arena with many satellite males the relative copulation frequency of satellites was supposed to be low. She further supposed that small arenas were formed when neighbouring large arenas had a maximum size. This was determined by two factors with opposite effects, namely a preference of independent males to settle on large arenas, and a high level of aggression of resident males towards marginal males on those arenas. Thus, according to HOGAN-WARBURG, in a given locality, changes in the numbers of either satellite males or independent males or both, would influence the relative copulation frequency of satellite males. An increment in the number of satellites would result in a decrement in their copulation frequency, an increment in the number of independent males would result in either a decrement or an increment, depending on the size(s) of the arena(s), in their copulation frequencies.

This explanation cannot be fully satisfactory, since the important question remains unsolved, and that is *why* the relative copulation frequency of satellites is negatively influenced by an increase in the number of satellites. This question can be regarded as a special case of our initial question: the negative correlation between relative frequency and copulation frequency.

The remaining criticism of HOGAN-WARBURG's explanation touches upon the value of her evidence for it. This evidence was based upon differences between two small arenas in one locality, and one large and one small arena in another locality (Table 43). In the first locality the number of satellites was relatively low, in the second relatively high, particularly on the small

TABLE 43

Density and relative copulation frequency of satellite males on four arenas in two different localities

		Numbers of males				copulations		on both arenas in one locality	
population	arena	res	marg	sat	% of sat	total	% by sat	% of sat	% of sat cop.
Schier *)	AH	5	9	5	26	32	41	20	28
	RW	5	9	4	22	39	18		
O.P. **)	large	19	13	23	42	53	4	39	7
	small	8	13	17	45	8	25		

*) between May 4 and May 17 (1960) **) between May 16 and May 28 (1962). (After HOGAN-WARBURG p. 187).

arena. However, the observations in the different localities were made in different parts of the season. Now my own observations on one arena in different seasons (1968, 1969) showed that the relative copulation frequency of satellites depended on the time of the season (Table 44). During the first half of the season (corresponding with HOGAN-WARBURG's observations in the first locality) satellite males copulate relatively often; during the second half (corresponding with the observations in the second locality) copulations of satellite males occur seldom. Thus, the differences HOGAN-WARBURG found between the relative copulation frequencies were probably an effect of the season.

TABLE 44

Seasonal differences in the relative copulation frequency of satellite males

	copulations 1968			copulations 1969			copulations total		
period	total	sat	% by sat	total	sat	% by sat	total	sat	% by sat
15/4-30/4	40	11	28	40	5	12	80	16	20
1/5-15/5	5	1	20	15	3	20	20	4	20
16/5-31/5	46	4	9	24	2	8	70	6	9
1/6-15/6	10	0	0	21	0	0	31	0	0

I found no support for HOGAN-WARBURG's suggestion concerning the control of the size of an arena. I could not demonstrate differences between large arenas and small ones in the number of marginal males (preference of independent males to settle on large arenas) and in the number of attacks on marginal males (aggressive level of resident males on large arenas). To illustrate this, data of 5 continuous observations (2 hours), collected on

5 different arenas within a period of 10 days, are given in Table 45. In this table the number of resident males is compared with: (i) the number of visits of marginal males during 2 hours, (ii) the mean number of attacks (per resident male) on marginal males during 2 hours, and (iii) the mean number of attacks of resident males on marginal males per visit of 100 minutes of a marginal male. None of these parameters appeared to be correlated with arena size. Thus, my data do not confirm HOGAN-WARBURG's suppositions regarding the control of arena size.

TABLE 45

Visits of marginal males and attacking rate towards marginal males in relation to arena size

arena	number of res males	I	II	III
A	28	18	2.3	48.6
B	12	28	0.3	1.3
C	12	26	0.3	1.5
D	9	65	17.0	30.9
E	4	20	11.7	28.3

5 continuous observations (2 hours) collected on 5 different arenas within a period of 10 days.

I number of visits of marginal males during 2 hours.

II mean number of attacks (per resident male) on marginal males also during 2 hours.

III mean number of attacks of resident males per visit of 100 minutes of a marginal male.

I want to postulate now an alternative hypothesis, based upon the circumstances in which I observed high copulation frequencies of satellite males, namely (i) during the early part of the season, (ii) on just established arenas, and (iii) after changes in the occupation of residences. Furthermore I had the impression that after disturbances on the arena (*e.g.* by catching) the relative copulation frequency of satellite males also increased. I gave above quantitative evidence for the first (i) statement (cfr. Table 44); the evidence for the second (ii) and third (iii) statements refers to qualitative observations.

A low number of stable relations between resident males is characteristic of all circumstances mentioned in the previous paragraph. At least some of the resident males were absent on the previous days on one or another particular residence and/or on the arena. This hinders a proper distinction between territorial and non-territorial males. So, one would expect that the number of attacks on non-territorial males is more like that on territorial males than in the situation with many stable relations between resident males.

To test this supposition I calculated for resident males, marginal males, and satellites per visit of 100 minutes the mean number of times they were attacked by a resident male during different parts of the season. Figure 24 shows that both marginal males and satellites were attacked more often during the end of the season (many stable relations) than in the early part of it (fewer stable relations), while resident males were attacked at a relatively constant rate, less often than marginal males, particularly during the end of the season. Pilot-observations on just established arenas suggested that here the number of attacks on non-territorial males is low. Furthermore I had the impression that after changes in the occupation of residences the number of attacks on resident males increased. Thus, in all situations with a low number of stable relations the proportions of attacks directed towards non-territorial males is lower than in situations with a high number of stable relations.

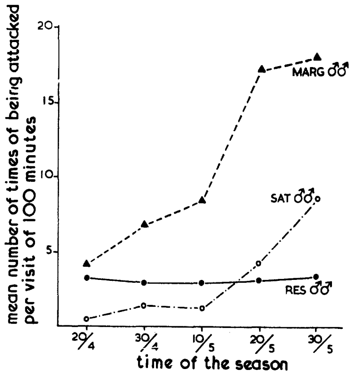

Fig. 15. Mean number of times of being attacked by a resident male for resident males, marginal males, and satellite males per visit of 100 minutes during different parts of the season.

It is plausible that the relative copulation frequency of satellite males largely depends on the number of attacks directed towards them. This might be regarded as the explanation of the low copulation frequency of satellites on arenas with many stable relations.

The growth of an arena is probably influenced by the number of attacks directed towards marginal males. Arenas with many stable relations between resident males, among which arenas existing for many years occupy an important place, seldom grow in size.

Thus, when in a given season the influx of new independent males (not present during previous seasons) is large, we can expect the establishment of new arenas without stable relations. On those arenas satellite males have many opportunities for copulating. For this reason the relative frequency of satellite genotypes will be increased in the next season. When the influx of new independent males is small, only the successful arenas of the previous year will be maintained. Because of the stable relations on these arenas satellite copulations will be rare. In this case the relative frequency of satellite genotypes will be diminished in the next season. So, the polymorphism in the Ruff may be due to selection of varying direction (cfr. HALDANE & JAYAKAR, 1963).

In fact this control mechanism only depends on the influx of new independent males. This implies that the proportion of satellite males in a population is not kept constant under all circumstances. In the case of a sudden increase or decrease in the numbers of independent males only, and in the case of a sudden increase in the numbers of satellites only, the ratio between both categories can be immediately corrected. However, in the case of a sudden increase or decrease in the numbers of both independent- and satellite males and in the case of a sudden decrease in the numbers of satellites only, the ratio between both categories will be thrown out of balance for a long period. An increase in the number of both categories will result in an increase in the relative frequency of satellite males (i); a decrease in the numbers of both categories in a decrease in the relative frequency of satellites (ii); and a decrease in the number of satellites only will result in a decrease in their relative frequency (iii). The first mentioned change (i) can be corrected in the next season after a small influx of new independent males (stable relations). The second (ii) and third (iii) deviations can only be corrected after a large influx of new independent males(also in the next season).

Thus, an important implication of this hypothesis is that independent males are favoured during periods with low numbers of male Ruffs (protection of mating places), and that satellites are favoured during periods with high numbers of males (protection of gathering of females). This favouring might enlarge the total reproductive output of the individuals in the population, since in small groups of males (females relatively common) the number of mating places might restrict the number of fertilized females, and in large groups (females relatively rare) the number of females might restrict the total number of copulations.

SUMMARY

In the Ruff two groups of males can be distinguished: independent males and satellite males. This classification is based upon differences in territoriality and behaviour, and is highly correlated with differences in the nuptial plumage. Independent

males are mostly dark coloured; their behaviour contains much fighting and related activities. They can be subdivided into resident males and marginal males. Resident males defend territories (residences), marginal males do not. Satellite males are mostly white. They behave peacefully and do not defend a territory. Satellite males have access to the residences on an arena (cfr. HOGAN-WARBURG, 1966).

In this study an attempt has been made to throw some more light upon the behavioural dimorphism (independent males *versus* satellites). On the one hand I tried to analyse the causation of this phenomenon, on the other hand I was interested in its biological significance. I have tackled these problems by means of an examination of film material, and by a quantitative study of the behaviour on different arenas (leks) in the field.

The film supplied me with detailed data about the behaviour of resident males, satellite males, and females in different external situations. On the basis of these data it was possible to analyse the temporal associations between the various behavioural units, for this purpose divided into "postures", "locomotion sequences", "action sequences", and "actions". The observed relations were largely similar for the three categories of individuals.

For this reason I was able to compose one model for the hypothetical causal mechanism underlying the behaviour of resident males, satellite males, and females. The display of postures was supposed to be controlled by the values of two variables, the display of the other units by the value of the same variables and directly by the external situation. The values of both variables depended on external stimuli and on the internal situation (partly determined by previous external stimulation). I could not obtain evidence for the existence of different mechanisms underlying the different groups of behavioural units serving one function, such as aggression, flight, and sex. These groups of behavioural units were fully integrated in the entire causal system. They each appeared at distinctive combinations of values of both variables. Aggressive and sexual behaviour appeared each at only one cluster of combinations, however, protective behaviour appeared at three clusters. The suitability of the drive concept for both variables has been discussed.

Normal behaviour of the three categories distinguished seemed to correspond to category-specific ranges of both variables. Female behaviour represented the one extreme, resident male behaviour the other one, and satellite behaviour was mainly intermediate. This intermediate behaviour has been ultimately ascribed to the light plumages of satellites and the genetical factors connected with that; the lack of a territory and distinct components in the behaviour of resident males towards satellites have also been emphasized as causal factors.

I presented arguments for the hypothesis that the status (independent or satellite) of an individual depends on genetical and environmental factors. The importance of genetical factors appears from the correlation between behaviour and plumage colour. The influence of the environment follows from (a) the inconstancy of the status of some individuals (particularly young ones), and (b) the relation between status of an individual and plumages of the other individuals present on the same arena.

It has been emphasized that some of the plumage colours occur exclusively in satellite males (satellite plumages), and others exclusively in independent males (independent plumages). Males with untypical plumages (intermediate colours) do not necessarily belong to one and the same category. They generally belong to the independent category when there are many males with satellite plumages on the arena, and relatively often to the satellite category when independent plumages are common. This phenomenon could not be ascribed to differential reproduction in previous seasons; it seemed to be connected with migration and changes of status, probably caused by low copulation frequences.

It is argued that males with independent plumages are homozygotes with respect to a particular gene, that males with satellite plumages represent the same condition but with alternative alleles, and that males with untypical plumages are heterozygotes. This implies that both the behaviour and the plumage are influenced by one pair of genes (pleiotropy).

Resident males can enlarge their reproductive output when tolerating satellite males on their residences in particular situations. The presence of satellite males on residences promotes the attraction of females. However, the presence of satellites has no influence on the duration of female visits, moreover, it has a negative effect on the copulation frequency of resident males. It could be demonstrated that the behaviour of resident males towards satellites is either tolerant or intolerant. Intolerant behaviour occurs when the resident male acquires a high density of female visits on his residence; it also occurs during and after high copulation frequencies of the male concerned. In all other circumstances tolerant behaviour will be shown. Both kinds of behaviour regularly alternate with a period of some days up to some weeks. This causes a large fluctuation in the density of satellite visits to the residence. The density of female visits also fluctuates, but less extremely.

The other factors influencing female and satellite visits to residences have been analysed. This enabled me to formulate a model by which the oscillations in the densities of female and satellite visits could be simulated. Furthermore the effects of satellites on copulating of resident males could be studied. Satellite males appeared to play a very important role. A resident male cannot attract enough females for copulating without co-operation with satellites. The copulation success also depends on the tactics of the resident male, particularly on the adjustment of the tolerant-intolerant transition. Furthermore the degree of intolerance plays an important role.

In the Ruff we are probably concerned with a balanced polymorphism. The genetical diversity may be a consequence of superiority of heterozygotes (males with untypical plumage colours). Another explanation is provided by the mutual dependence between independent males and satellites. It is likely that the fitness of individuals of either category changes during oscillations of their relative frequencies, because of the change in the effectiveness of the co-operation with the other category.

It is suggested that the success of satellite males on an arena is negatively correlated with the number of stable relations between resident males. In the early part of the season, on recently established arenas, and after changes in the occupation of residences the copulation frequency of satellite males is high. This phenomenon is probably caused by the low number of attacks on non-territorial males in such situations. The high number of attacks on marginal males in the other situations implies that arenas seldom grow when stable relations are common. Hence the relative frequencies of independent males and satellites are supposed to be controlled by the influx of new independent males, and thus by the establishment of new arenas. This hypothesis implies that independent males are favoured during periods with low numbers of males, and that satellites have the advantage when there are many males.

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RÉSUMÉ

Chez le Chevalier Combattant, on peut discerner deux groupes de mâles: les mâles indépendents et les mâles satellites. Cette classification est basée sur les différences en occupation du territoire et en comportement, auxquelles sont étroitement liées les différences en plumages nuptiaux. Les mâles indépendents sont le plus souvent foncés; leur comportement se compose en grande partie de combats et d'actions similaires. Ce groupe de mâles peut être subdivisé en mâles résidants et en mâles marginaux. Les premiers défendent un territoire (résidence); les derniers ne le font pas (encore). Les mâles satellites ont en général un plumage blanc. Ils se tiennent paisibles et ne défendent pas de territoire. Par contre, ils ont l'accès libre aux résidences à une arène (cfr. HOGAN WARBURG, 1966).

L'objet principal de cette étude a été la dimorphie en comportement (les différences entre les mâles indépendents et satellites). Je me suis intéressé à la causation de ce phénomène, ainsi qu'à sa signification biologique. J'ai traîté ces problèmes en examinant des films et en étudiant, d'une manière quantitative, le comportement sur le terrain, à des arènes différentes.

Les pellicules m'ont fourni des données très détaillées sur le comportement des mâles résidants, des mâles satellites et des femelles, en différentes situations externes. Ces données m'ont servi de base pour l'analyse des associations temporelles entre les diverses unités de comportement. (Pour cela, ces unités sont subdivisés en "attitudes", "series de locomotion", "séries de mouvements" et "mouvements"). Les relations trouvées sont laregments semblabes dans les trois catégories d'individus.

Ce fait m'a permis de composer un modèle mathématique d'un seul mécanisme causal hypothétique, pour expliquer le comportement des trois catégories d'individus. L'attitude de l'oiseau est supposé sous le contrôle des valeurs de deux variables; l'apparition des autres unités est déterminée par des valeurs des mêmes variables et, en façon directe, par la situation externe. Les valeurs des deux variables dépendent aussi bien de la stimulation externe que de la situation interne (la dernière étant partiellement déterminée par la stimulation externe précédente). L'apparition des complexes d'unités de comportement avec une fonction biologique (comme le complexe agressif, sexuel, *etc.*) ne peut pas être attribuée à des mécanismes causaux particuliers. Ces groupes d'unités de comportement sont entièrement intégrés dans le mécanisme total: ils apparaissent avec certaines combinaisons des valeurs des variables. Le comportement agressif et sexuel apparaissent chacun avec un seul groupement de combinaisons des valeurs, tandis que le comportement protectif se manifeste avec au moins trois groupements de combinaisons. Aussi, la praticabilité du concept de „drive" aux deux variables est mise en discussion.

Le comportement normal de chacune des trois catégories d'individus est caractérisé par une certaine limite de variation des deux valeurs, qui est donc spécifique pour cette catégorie. Ainsi, le comportement des femelles peut être représenté sur l'une des extrémités, celui des mâles résidants sur l'autre, et le comportement des mâles satellites se situe entre les deux. La position intermédiaire de ce comportement a été ultérieurement attribuée à la couleur nuptiale claire des mâles satellites et aux facteurs génétiques liés à celle-ci. En plus, j'ai avancé comme autres facteurs causaux, le manque de territoire et certains components distincts dans le comportement des mâles résidants envers les mâles satellites.

Le rôle d'un individu (indépendent ou satellite) dépend vraisemblablement aussi bien des facteurs génétiques que de l'environnement. L'importance des facteurs génétiques se manifeste par la correlation entre le comportement et les couleurs nuptiales. L'influence du milieu peut être déduite premièrement (a) de l'instabilité du rôle de certains individus (particulièrement des jeunes) et en second lieu (b) de la relation entre le rôle d'un individu et les couleurs nuptiales des autres individus, présents a la même arène.

J'ai indiqué que certaines couleurs nuptiales apparaissent uniquement chez les mâles satellites (plumage de satellite), et certaines uniquement chez les mâles indépendents (plumage d'indépendent). Dans les deux catégories de mâles, on trouve, pour le reste, des mâles autrement colorés (avec plumages atypiques, couleurs intermédiaires). Les mâles aux couleurs nuptiales atypiques ont en général le rôle indépendent quand il y a beaucoup de mâles aux plumages de satellite. Lorsque les mâles aux plumages d'indépendent sont en majorité, les mâles aux couleurs atypiques obtiennent le rôle satellite. Cette relation entre le rôle d'un individu et les couleurs nuptiales des autres, ne peut pas être expliqué par une réproduction différentielle en saisons précédentes. Le phénomène semble être lié aux migrations et aux changements de rôles, qui ont, à leur tour, pour cause probable des fréquences de copulations (trop) basses.

J'ai souligné la possibilité que les mâles aux plumages d'indépendent soient homozygotes pour un gène particulier, et que les mâles aux plumages de satellite représentent la même condition, mais avec les allèles alternatifs. Les mâles aux plumages atypiques seraient hétérozygotes. Ceci implique que le comportement aussi bien que la couleur nuptiale, seraient influencés par une seule paire de gènes.

Les mâles résidants peuvent aggrandir leur succès réproductif en laissant aux mâles satellites l'accès libre à leurs résidences en certaines situations. La présence de mâles satellites à une résidence augmente l'attraction des femelles. Par contre cette présence de mâles satellites n'influence pas la durée des visites des femelles, réduit même les chances de copulation des mâleses résidants. Pour le mâle satellite, l'accès à une résidence dépend du comportement du mâle résidant. Celui-ci se montre intolérant lorsqu'il acquiert de hautes densités de visites de femelles, et également, lorsqu'il a obtenu lui-même de hautes fréquences de copulations. Dans toutes autres circonstances, le mâle residant reste tolérant. Ces deux types de comportement (tolérance, intolérance) alternent régulièrement. avec une période de quelques jours jusqu'à quelques semaines. Ceci provoque une forte fluctuation de la densité des visites des mâles satellites aux résidences. La densité des visites des femelles varie de la même façon, mais moins fort.

J'ai analysé également les autres facteurs qui influencent les visites des femelles et des mâles satellites. Ainsi, j'ai pu élaborer un modèle mathématique qui simule les oscillations des densités des visites des femelles et des mâles satellites. En outre, j'ai su étudier l'influence des visites des mâles satellites sur les chances de copulation des mâles residants. Les mâles satellites semblent jouer un rôle très important. Un mâle résidant, qui ne coopère pas avec des mâ satellites, ne peut pas, à lui seul, attirer suffisamment de femelles pour accoupler. Ainsi, le succès de copulation d'un mâle résidant, dépend de sa tactique, c'est-à-dire, de la façon de laquelle le mâle résidant ajuste la transition tolérance-intolérance à la situation à sa résidence, et aussi, du degré auquel il se montre intolérant.

Chez le Chevalier Combattant, nous avons probablement à faire à un polymorphisme balancé. L'hétérogénéité peut être maintenue par la superiorité des hétérozygotes (les mâles aux couleurs atypiques) mais aussi par la dépendance mutuelle des mâles indépendents et satellites. Il est probable que la valeur sélective d'un individu de chacune des deux catégories varie avec les oscillations de leurs fréquences relatives à cause de la modification dans l'efficacité de coopération.

J'ai suggéré que le succès réproductif des mâles satellites serait inversement proportionnel au nombre de rélations fixes entre les mâles résidants à une arène. La fréquence de copulation des mâles satellites est élevée au commencement de la saison, puis aux arènes qui viennent d'être établies, et aussi après des changements dans l'occupation des résidences. L'explication de ce phénomène peut être donnée par le fait que, dans les trois situations nommées, les mâles, qui n'ont pas de territoire, sont très peu attaqués par les mâles résidants. Dans les autres situations, les mâles marginaux sont fortement attaqués, ce qui implique que les arènes ne s'aggrandissent pas quand les relations entre les mâles résidants sont fixes. Ainsi, les fréquences relatives des mâles indépendents et des mâles satellites paraissent sous le contrôle de l'affluence de nouveaux mâles indépendents, et donc de l'établissement de nouvelles arènes. Cette hypothèse inclue que les mâles indépendents sont favorisés lorsqu'il y a de grands nombres de mâles, et que les mâles satellites sont avantagés lorsque le nombre de mâles est plutôt restraint.