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A CORRELATION ANALYSIS OF THE DAILY DISTRIBUTION OF DISPLAYS AND SEXUAL BEHAVIOURS IN SEMI-WILD MALLARDS *Anas platyrhynchos*

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Aspirant F.N.R.S.

This paper describes the daily and seasonal variations of the social displays and sexual behaviour exhibited by a population of semi-wild mallards living in the natural reserve Le Zwin (Belgium). The seasonal variations already observed by Weidmann (1956) and Lebret (1961) are confirmed. It is shown that the social displays present a daily bimodal activity pattern with higher activity in the early morning and late afternoon. Rather surprisingly the copulations and related behaviour present a different daily distribution and occur preferably around noon. Some implications of these differences in daily distribution are discussed. The number of males in the pond is shown to be positively correlated with the frequency of social displays observed thus indicating that one of the most important activities of swimming mallards is to engage in social display. These facts are in good agreement with observations realized on another Anas species, the Green-winged Teal (*Anas c. crecca*). A possible effect of the time of sunrise on the daily activity pattern is also suggested. No short-term periodicity can be detected in the general activity observed on the pond by the use of the auto-correlation function. The cross-correlations are shown to be a useful tool for behavioural studies. Finally some methodological remarks are formulated concerning a method for data filtration which prevents the occurrence of some meaningless correlations.

INTRODUCTION

Many animal species have been shown to exhibit a bimodal pattern of activity with activity peaks occurring in the early morning and late afternoon (Aschoff, 1966). In the mallard, Winner (1959) has shown the existence of a periodicity in the field-feeding activities as measured by the number of flights from the resting areas on water to the upland fields where the birds feed. He presented quantitative evidence demonstrating that the flights occur essentially at dawn and at dusk. In a later paper he further showed that the bimodal activity pattern persists in birds kept in a controlled environment with constant light intensities during a 10-hour photoperiod (Winner 1972).

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[1] I am indebted to Professor E. Schoffeniels for his encouragements and his interest in my work. This research was partially supported by a Camille Hela grant to J. Balthazart and by a grant n° 790 from the *Fonds de la Recherche Fondamentale collective* to Professor E. Schoffeniels. I acknowledge also the help of Professor U. Weidmann (University of Leicester) who corrected the manuscript and made many fruitful suggestions.

During studies on the hormonal control of the behaviour in male domestic ducks, I have noticed a considerable variation in plasma testosterone levels with peaks in the early morning and to a lesser extent in the late afternoon (unpublished results). As testosterone injections are known to elicit displays and sexual behaviours in mallards (Etienne and Fischer 1964) and in domestic ducks (Balthazart 1974) I wondered if the changes in the plasma testosterone levels could not be paralleled by changes in sexual and display behaviours. Little is known on the daily distribution of these activities in ducks. Weidmann (1956) and Raitasuo (1964) gave some attention to this problem. Raitasuo (1964) pointed out that all activities of the mallard including displays are regulated by a short-periodic rhythm which divides the day into numerous phases of high activity (lasting 45 to 75 minutes) followed by rest periods of 30 to 45 minutes. However, no information can be found on a truly daily rhythm except in a graph of Weidmann (1956, p. 240) showing the activities of one pair of ducks during a single day. It was consequently decided to undertake the present study to provide information on the daily sexual and display activity pattern of the mallard.

MATERIAL AND METHODS

All the observations reported here were carried out during the months of January to March 1972 in the Natural Reserve : Le Zwin at Knokke (Belgium)[2]. During that period, the population of semi-wild resident mallards is joined by a large number of birds overwintering in the Reserve. An observation area (more or less 80 × 80 m) was defined which comprised a pool (about 30 × 50 m), a small wooded area and a piece of meadow. The whole area has been man-made with a view to providing adequate conditions for ducks with easy observation by visitors. For 10 days (± 98 hours)[3] I observed all the male mallards present in this area from dawn to the end of the afternoon (more or less half an hour before dusk) at the moment when additional food is distributed to the birds, this latter fact causing a great disturbance and actually marking the end of the day.

Observations were made continuously from dawn to 11.15 a.m. and for every other 15 minute period from 11.15 a.m. to the end of the day. I recorded the frequency of occurrence of different behaviour patterns during each 15 min period. I only considered the behaviour elements performed by males in the defined area, whatever their number. Observations were recorded on magnetic tape with a portable

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[2] I acknowledge here the observational facilities provided at the Reserve by MM. L. Lippens and G. Burgrave respectively owner and conservator of the Reserve.

[3] The following will be referred to as the days of observation : day 1 : 23 Jan; day 2 : 24 Jan; day 3 : 25 Jan; day 4 : 8 Feb; day 5 : 9 Feb; day 6 : 22 Feb; day 7 : 23 Feb; day 8 : 8 March; day 9 : 9 March and day 10 : 23 March.

recorder and later transcribed on paper. At the beginning and the end of each observation period of 15 min I also recorded the number of males present in the observation area and those in the water or on land[4]. For 5 days, pictures were taken of the observation area each 15 minutes and later the number of birds present in the pictures were analysed. The two methods gave almost identical results so that only scores obtained by direct observation will be discussed here. In the following treatment of the data, only observations ranging from 8.00 a.m. to 5.00 p.m. will be used as this is the longest period of recording it has been possible to use for all the days (i.e. it is the length of the shortest observation).

The analysis of variance was performed with a Diehl Algotronic calculator while the auto- and cross-correlations were computed by an IBM 370-198 computer using a program written in P.L.1. The behaviour patterns which were scored belong to two main categories already recognized by Weidmann (1956):

- The display activities: I recorded separately Head-Flick (HF)[5], Introductory Shake (IS), Grunt-Whistle (GW), Head-up-Tail-up (HU), Nod-Swimming (NS) and Down-UP (DU).
- The displays accompanying copulation in which I distinguished Rapes (RA), Pumping (PU), Grasping the female's neck feathers (GR), Mounting the female (MO), Copulation (CO), Bridling (BR) and post copulatory Nod-swimming (NO).

The description of these well-known behaviour patterns can be found in Lorenz (1941), Weidmann (1956), Johnsgard (1965) and MacKinney (1969).

PRELIMINARY PROBLEMS

EXISTENCE OF "NATURAL" GROUPS IN THE REPRODUCTIVE ACTIVITIES

For a long time, 3 main groups have been recognized in the reproductive activities of the mallard duck (Weidmann 1956). They are:

- The social displays which include the shakes (Introductory-Shakes, Head-Shakes, Head-Flicks) and 4 major displays (Grunt-Whistle, Head-up-Tail-up, Nod-Swimming and Down-Up).
- The displays involved more directly in pair formation or directed courtship (Von de Wall 1965) including leading and Mock-preening or pseudo-preening.
- The displays accompanying the copulation: pumping, grasping the female's neck feathers, mounting, copulation, bridling and post-copulatory Nod-Swimming.

[4] Almost all the reproductive activities happen in the water; on land, the birds feed or sleep most of the time. So for this study I shall almost exclusively take into account the number of birds seen in the water.

[5] The abbreviations in brackets will be used in this paper.

However these groups have been shown not to be absolutely homogeneous in all their aspects. For example, De Lannoy (1967) has shown that the down-up is specifically elicted by the presence of a rival male and has suggested that this display is aggresively motivated (this probably being untrue for the other major social displays).

All the behaviour patterns I have studied belong to the social displays and to the displays related to copulation. I have at first wondered if all the behaviour elements belonging to a given group have a similar distribution throughout the day. Therefore I have computed the correlation between the frequency of each behaviour and the frequency of each other behaviour as well as the correlation of each behaviour with the total number of behaviours of a given group for the different hours of the day. The results are expressed in Table 1.

It is clear that in all cases (except for RA) the daily variations of each display frequency are highly correlated with the variations of all the group[6,7]. Consequently it did not prove to be absolutely necessary to study further each display separately. Afterwards I have only kept two behavioural variables which are the sum of the social displays and the sum of the behaviours related to copulation and I will refer to them as "social displays" and "sexual behaviours". Rapes are not discussed separately because this type of behaviour is scarce in my observations (54 occurrences for about 10,000 behaviours observed).

EFFECTS OF MISCELLANEOUS PERTURBATIONS

As mentioned in the section "Material and Methods" the place chosen for the observations has the great advantage of gathering a large number of ducks in a place where they can be easily observed. However a problem has been raised by the fact that this place is in a park open to visitors who sometimes feed the ducks, causing an evident disturbance. Consequently, variations in the behaviour observed could have reflected the disturbances caused by the visitors. In order to discard this possibility I have recorded the occurrence of each visitor or group of visitors. So I have been able to test whether or not the visitors affect in any way the frequencies of social display and sexual behaviours or the number of males being in the water. In all my data I have verified whether the number of displays, sexual behaviours, males being in the water, increased or decreased when there was a disturbance during a given observation period of a quarter of an hour or if there had been a disturbance during the preceding period. I have further noted if the number of displays and sexual behaviours was higher or lower than the daily mean in the observation periods when

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[6] This would be expected as it is well known that all the behaviours in each group occur in a more or less rigid sequence.

[7] Correlations computed with the Spearman Rank Correlation coefficient furnish exactly the same results.

	social displays							displays related to copulation							
	HF	IS	GW	HU	NS	DU	sum		Pu	Ra	MO	Gr	CO	Br	NO	sum
HF	—	0.89	0.90	0.84	0.84	0.87	0.97	Pu	—	0.02	0.57	0.56	0.60	0.57	0.57	0.63
										NS	**	**	**	**	**	**
IS		—	0.93	0.75	0.75	0.83	0.93	Ra		—	0.00	0.02	0.00	-0.01	-0.01	0.15
											NS	NS	NS	NS	NS	NS
GW			—	0.77	0.76	0.82	0.94	MO			—	0.97	0.97	0.97	0.97	0.94
HU				—	0.98	0.86	0.86	Gr				—	0.98	0.97	0.97	0.94
NS					—	0.88	0.87	CO					—	0.99	0.99	0.95
DU						—	0.91	Br						—	1.00	0.95
sum							—	NO							—	0.95
								sum								—

TAB. 1. CORRELATION COEFFICIENTS OF EACH BEHAVIOUR PATTERN WITH EACH OTHER ACTIVITY AND WITH THE SUM OF THE GROUP TO WHICH IT BELONGS. Data are the frequencies for different hours of the day. Correlations have been computed on desautocorrelated series (see appendix B). Unless otherwise stated coefficients are significantly different from zero for $P < 0.001$. In the table: NS = Non significant, ** = $P < 0.01$

there was a disturbance and when there was a disturbance in the preceding period. Using a Binomial-test (Siegel 1956) no significant difference can be found in any case at the 5% level. Consequently I can reject the hypothesis that the daily variations of behaviour could be caused by the disturbances due to visitors. I want further to mention that as the observations were carried out during the winter, only a few visitors were observed in the reserve (40 occurrences for the 10 days together with a maximum of 8 distinct occurrences on a single day). This fact further reduces the probability that the variations of behaviour could be caused by the occurrences of visitors.

SEASONAL VARIATIONS

These observations were gathered during a 3-month period. During this time, important variations occurred in the number of ducks being in the reserve as well as in the activity of each duck. These variations are presented in Figure 1.

Figure 1A shows that the daily mean number of males recorded in the pond at the end of March is less than a quarter of those recorded in January. This is essentially the result of the departure of the ducks from their wintering area at the reserve to their northern reproductive sites. It can also be observed that the daily mean of reproductive behaviours present important variations with the season (Fig. 1A) and furthermore that these variations are not only the result of the decrease in the number of males (Fig. 1B).

Here I shall only draw attention to the methodological implications of these seasonal variations superimposed on the diurnal variations which are under study. In each subsequent treatment of the data care has been taken to isolate the proper effects of the diurnal variations from the seasonal ones. As the social display frequencies and number of males were extremely low at the end of March, the 10th day of observation has not been considered in most of the subsequent treatment for these 2 variables.

RESULTS

ANALYSIS OF VARIANCE

The first aim of my investigation is to discover if the 3 variables i.e. the social displays, sexual behaviours and number of males in the pond are significantly dependent on the hour of the day and secondly on the season. This has been tested using a 2-way analysis of variance (Dagnelie 1970). Table 2 summarizes the results of the analysis. The analysis demonstrates a highly significant effect of the hour of observation on the frequencies of social displays and sexual behaviours. The effect is very highly significant on the number of males. Similarly the seasonal effect is very highly significant on the social displays, the sexual behaviours and the number of males.

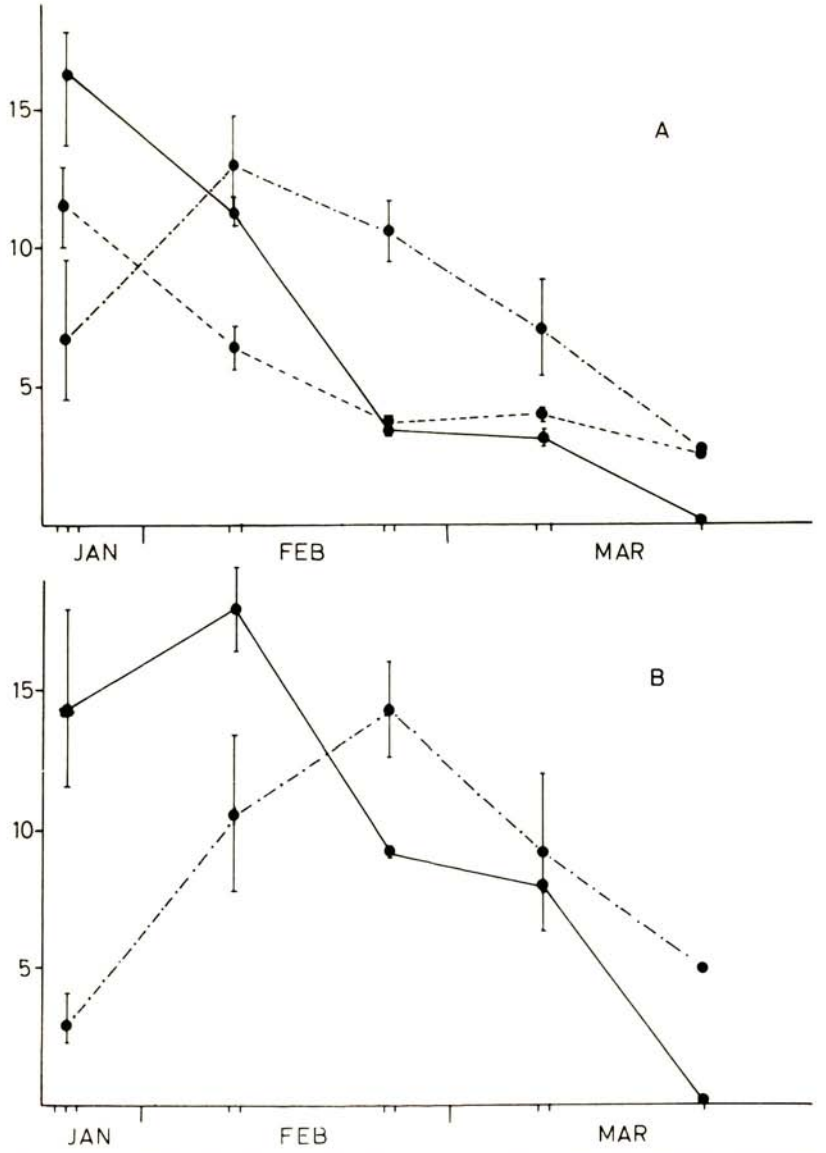

FIG. 1. A. SEASONAL VARIATIONS OF THE SOCIAL DISPLAYS, SEXUAL BEHAVIOURS AND NUMBER OF MALES. Data are the sums of all the observations at different hours on a given day. Mean and range are given for each series of consecutive days of observation. ——: social display frequencies × 10^{-2}; -·-·-: sexual display frequencies × 10^{-1}; – – –: number of males in the pond. Abscisses: time in month, ordonates: frequencies as explained above — B. SEASONAL EVOLUTION OF THE SOCIAL DISPLAYS × 10^{-1} (——) and sexual behaviours × 0,5 (-·-·-) FREQUENCIES DIVIDED BY THE NUMBER OF MALES SCORED IN THE POND. Data are the sum of the observations on a given day. Mean and range are given for each series of consecutive days.

At this point, it is necessary to describe how the two sources of variations affect the 3 variables. This has been done using the method of the least significant difference (Dagnelie 1970) and the results are expressed in Figures 2 and 3. It immediately appears that social displays are significantly more frequent in the early morning and late afternoon than at noon, while on the contrary the sexual behaviours and the copulations occur preferably around noon. Important peaks of

variable	source of variation	df	sum of squares	mean square	F	P
social displays	hour	23	117,902.7	5,126.2	2.45	$p < 0.005$
	season	8	139,174.2	17,396.8	8.03	$p < 0.0005$
	total	184	385,438.7	2,094.6		
sexual behaviours	hour	23	775.7	33.7	2.11	$p < 0.005$
	season	9	558.0	62.0	3.90	$p < 0.0005$
	total	207	3,302.9	15.9		
number of males	hour	17	2,239.4	131.7	5.75	$p < 0.0005$
	season	8	1,940.7	242.6	10.6	$p < 0.0005$
	total	136	3,117.1	22.9		

TAB. 2. TWO-WAY ANALYSIS OF VARIANCE: EFFECTS OF TIME OF DAY AND SEASON ON SOCIAL DISPLAYS, SEXUAL BEHAVIOUR AND NUMBER OF MALES IN THE WATER. – Only 9 days are included in the analysis of social displays and number of males because data are too scarce on the 10th day for these variables. – Only 18 observations are available daily for the number of males to prevent duplication of the information provided by the scores before 11.00 a.m. (the end and the beginning of two adjacent periods of observations being confused).

social displays also occur at 11.00, 12.00 a.m. and 2.30 p.m. These peaks are however not statistically different from the low levels of activity observed around 1 p.m. because they are associated with too large standard errors. This essentially expresses the fact that some displaying activity is also observed at these times but it occurs quite irregularly with respect to intensity and time of occurrence. The variations in the number of males are rather similar to those of the social displays: more males are in the water in the morning and in the afternoon than at noon.

The analysis by the same method (least significant difference) of the second factor (seasonal effect) is presented in Figure 3. Here again the social displays and sexual behaviours showed a different seasonal distribution. Social displays decreased monotonously from January to March (being significantly more frequent in January than in late February and in March), while the frequency of sexual behaviours increased from January to mid-February and then only decreased (frequencies being significantly higher by mid-February than in January and in March). Here again the distribution of the number of males is similar to that of the social displays.

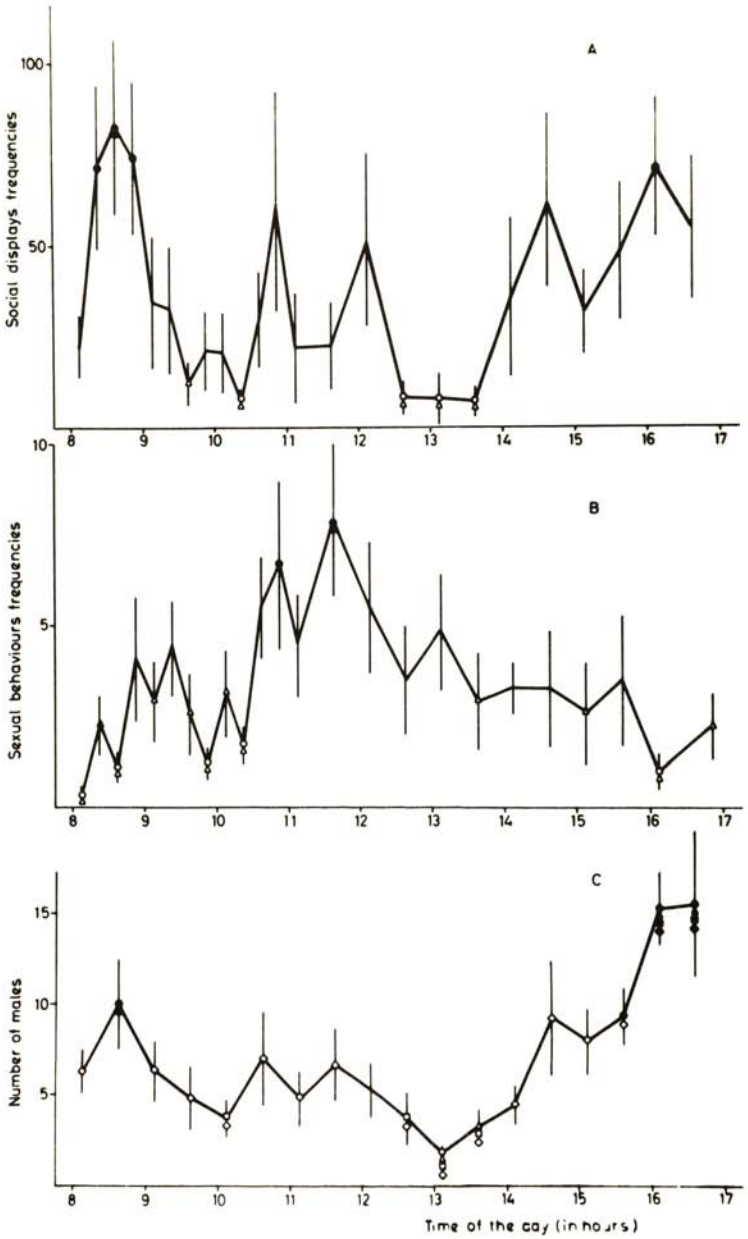

FIG. 2. EFFECTS OF THE HOUR OF THE DAY ON THE SOCIAL DISPLAYS (A), THE SEXUAL BEHAVIOURS (B) AND THE NUMBER OF MALES IN THE WATER (C). Mean $\pm$ 1 SE at a given hour for all days are presented. Large SE are partially due to the variation of the other factor (seasonal effect). All points indicated by a given open symbol are significantly lower than points indicated by the same closed symbol ($P < 0.01$ by the method of the least significant difference).

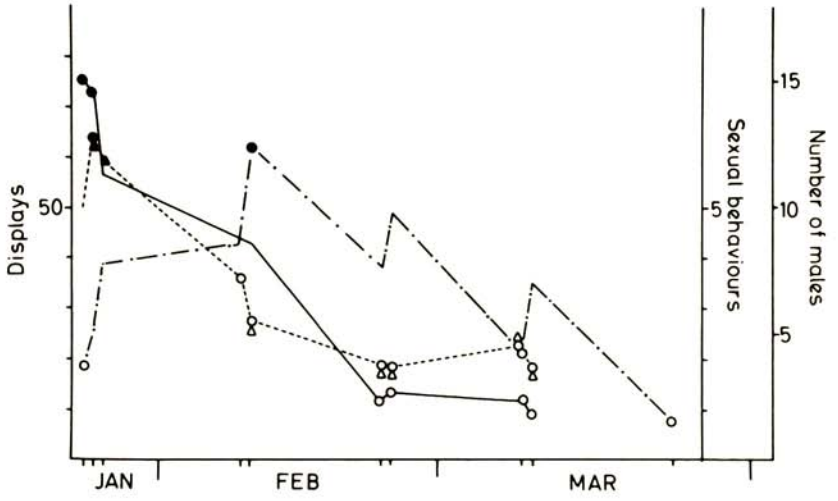

FIG. 3. EFFECTS OF THE SEASON ON THE SOCIAL DISPLAYS (——), THE SEXUAL BEHAVIOURS (–·–·) AND THE NUMBER OF MALES IN THE WATER (– – –). Mean of all the observations of each day are given. Points indicated by a given open symbol are significantly lower than the points indicated by the same closed symbol ($P < 0.01$ by the method of the least significant difference). Time in month is reported in the abscisses, the ordonates indicate the levels of the three variables studied.

RESEARCH ON SHORT-TERM RHYTHMS

The papers of Weidmann (1956) and Raitasuo (1964) claimed that the activities of a mallard show a short-term rhythm in which high-activity phases of 45-75 minutes were followed by rest periods (36-45 minutes). This led me to query if this type of short-term rhythm could be detected in the global activity of the whole population of ducks I had observed. This has been analysed by computing for each variable (social displays, sexual behaviours and number of males) the autocorrelation function of the data for each day separately. The method already used by Delius (1969) in a behavioural context is fully described in Bendat and Piersol (1971). The autocorrelation function describes the general dependence of the values of the data at one time on the values at another time. It is possible to compute this dependance (= correlation) for different time displacements. The plot of autocorrelation versus time displacement is called an autocorrelogram. A review of the applications of the analysis of time dependency in ethology can be found in Bercken (1974). In this case, the autocorrelation function has been computed for up to 6 unitary time displacements or lags in the positive and negative directions[8]. If the studied variables display a

[8] For these computations only one observation out of two was retained in the morning.

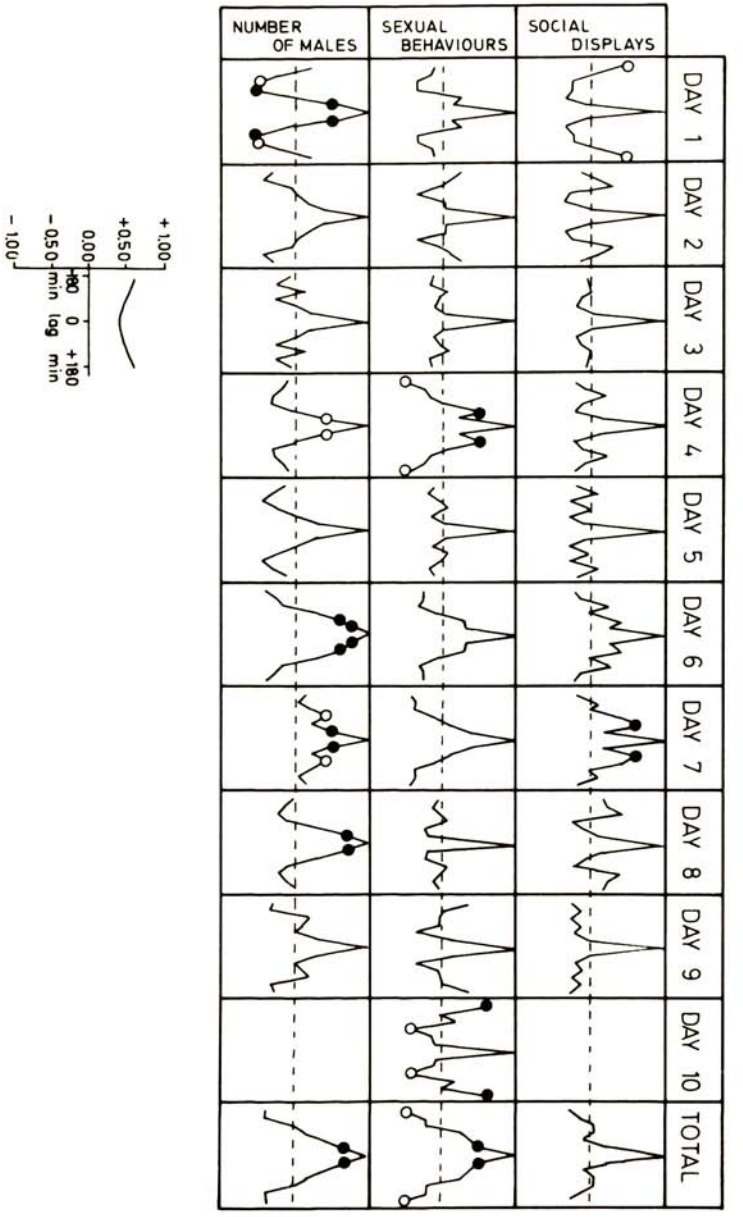

FIG. 4. AUTOCORRELATION FUNCTIONS FOR SOCIAL DISPLAYS, SEXUAL BEHAVIOURS AND NUMBER OF MALES BASED ON EACH DAY OF OBSERVATION AND ALSO ON THE TOTAL OF ALL THE OBSERVATIONS. The inset indicates the critical positive correlation coefficients for $p = 0.05$. In the main figure, black circles indicate correlations significantly different from zero for $p \leqslant 0.05$, the open circles indicate significant correlations for $p \leqslant 0.10$. In each square, ordinates indicate the level of correlation from +1.00 to −1.00, the abscisses show the different lags from −6 (−180 minutes on the left) to +6 (+180 minutes on the right).

short-term rhythm with a period ranging between 75 and 120 minutes, one could expect to observe a great dependence between the data separated by a corresponding lag (72-120 min i.e. a displacement of 2-4 units). Figure 4 shows that in fact this is not the rule. Almost no significant positive correlation appears at the predicted lag for any of the variables studied. Most of the positive correlations observed occur at lags of $\pm$ 1 unit (see for example the total of sexual movements and of the number of males, also the number of males on many days: day 1 - 6 - 7 - 8). These correlations at short lags reveal the existence of a tendancy in the corresponding data, i.e. that the data are not stochastic series but show only slow variations. In other words, the value of one variable is related to the values of the same variable half an hour before, that is to say for example that if the number of males in the water is high at a given time it is likely to be high half an hour later. This type of correlation is more frequent for the number of males than for the 2 behavioural variables indicating that the number of males in the pond tends to change more slowly than the behavioural frequencies. Except for these correlations at short lags, most of the other correlograms decrease in a continuous manner to a zero correlation with the increasing lags. A few correlograms suggest dependencies for the largest lags (social displays on day 7 and sexual behaviours on day 4 at a lag of 2 units, sexual bahaviours on day 10 at a lag of 6 units) however no conclusion can be drawn from these apparent exceptions.

The behavioural rhythmicity described by Raitasuo cannot thus be demonstrated for a population of mallards with the method used. Two main reasons could explain this failure. The first is a behavioural one. The observations were carried out during a period ranging from January to March. At that time it is known that the mallards which have spent the beginning of winter in a group in which they show a great synchrony of behaviour begin to live in heterosexual pairs, each pair showing its own activity rhythm (Raitasuo 1964). If this was the case during our observations it would then be normal that no short-term periodicity can be detected in data resulting from the observation of a large population of birds.

Methodological considerations could also explain our failure to detect the short-term periodicity. I have indeed used for this study a relatively large time unit (a quarter of an hour of observation for each half hour) as compared with the length of the series to be correlated (one day from 8 a.m. till 5 p.m., i.e. 18 periods of observation) and also with the periodicity to be detected (75-120 minutes according to Raitasuo). Consequently, the analysis which has been performed is rather rough and interesting features which could have been described with a

before 11.15 a.m. so that one observation of a quarter of an hour is available for each half hour throughout the day (see section Material and Methods). So each unitary time displacement corresponds to a displacement of half an hour in the data and a displacement of 6 units refers to a displacement of 3 hours in the data.

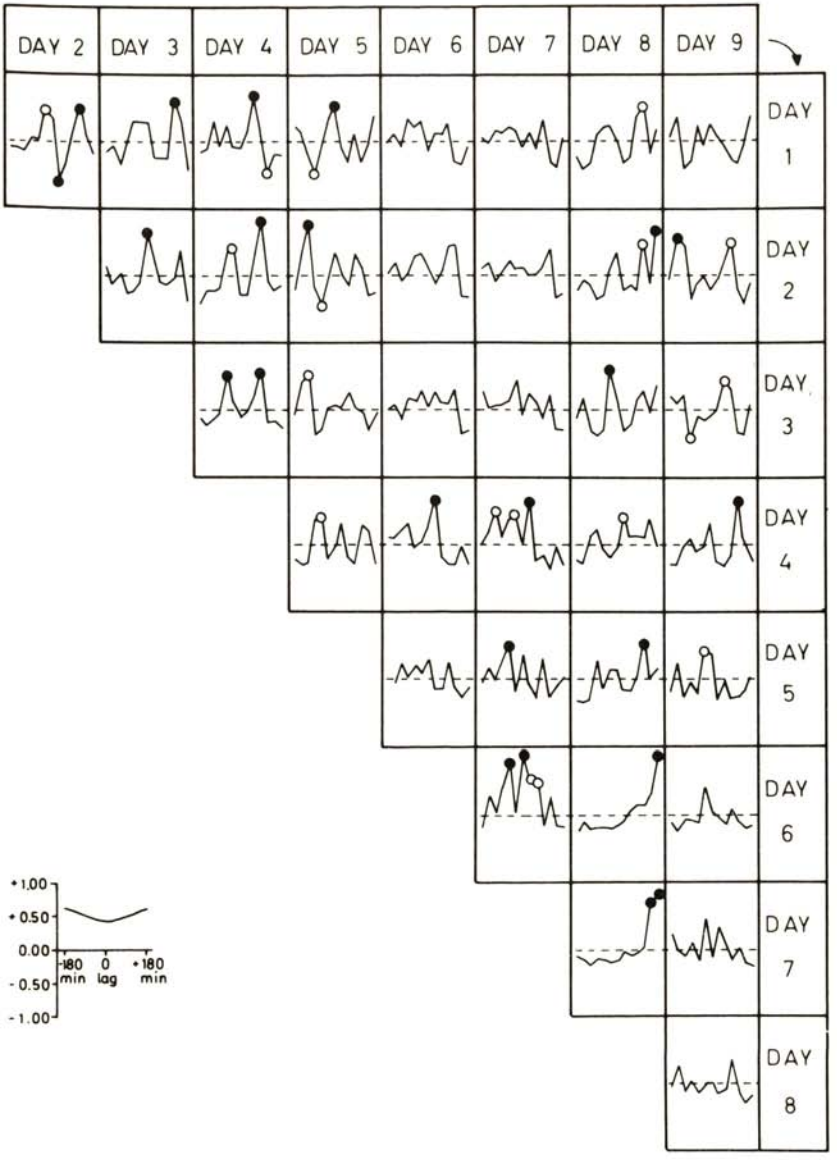

FIG. 5. CROSS CORRELATION FUNCTIONS FOR SOCIAL DISPLAYS COMPUTED FOR EACH DIFFERENT PAIR OF OBSERVATION DAYS, AFTER DESAUTO-CORRELATION OF THE SERIES (see text). See also legends of Fig. 4 for other comments.

shorter time unit have probably been missed. A study performed earlier in the season (in November-December when the birds live in groups) or on individual animals using a shorter time unit (2-5 minutes) might reveal interesting results concerning this problem.

CROSS-CORRELATIONS

The auto-correlation method used in the preceding section is in fact only a special case of the cross-correlation method in which two different series are correlated with a view to noting time-dependencies between them. I have used this method to solve two different problems. I have first checked if the daily variations described in section 2 were really the results of the fact that on each day separately the variables under study display the same variation. I have also demonstrated that the social display frequencies and the number of males show similar daily variations while the frequencies of sexual behaviours varies in a quite different way. The second problem was to show that there is a time-dependency between the two first variables while the third one is negatively correlated with the first two.

SIMILARITY OF THE VARIATIONS IN THE DIFFERENT DAYS

For each variable the cross-correlation function has been computed between each pair of different days of observation. As previously, the maximum relative time displacement of the series that has been used is a lag of $\pm$ 6 units that is to say $\pm$ 3 hours. The series have however been filtered (desautocorrelated) before the calculation to discard meaningless correlations (see the mathematical appendix B). I recall here that the cross-correlation describes the dependency between 2 time series for various relative displacements of the series. The cross-correlograms are therefore not symmetrical for negative and positive lags as the autocorrelation was, for it is not equivalent to have a shift of a series A relatively to a series B in one direction or in the opposite one.

The cross-correlograms between the different days of observation for the social displays, the sexual behaviours and the number of males are shown respectively in Figures 5, 6 and 7. I shall discuss separately the 2 behavioural variables and the number of males.

As expected the cross-correlograms between the frequencies on different days of social displays and of sexual behaviours show frequent positive correlations and rare negative ones. In fact 19 pairs of days are positively correlated for the social displays (Fig. 5) and 21 pairs for the sexual behaviours (Fig. 6) while only one pair of days is negatively correlated for social displays and 4 pairs for the sexual behaviours. This difference between the numbers of positive and negative correlations that occurs is very highly significant in the 2 cases ($P < 0.001$ binomial test in Siegel 1956). This high frequency of positive significant correlations is an indication of similarity between the daily patterns of activity in the different days. Two points however indicate that this similarity is not as strong as might be expected.

– Very few correlograms are symmetrical. Rare examples are the relation of displays on day 3 with display on day 4 and of sexual

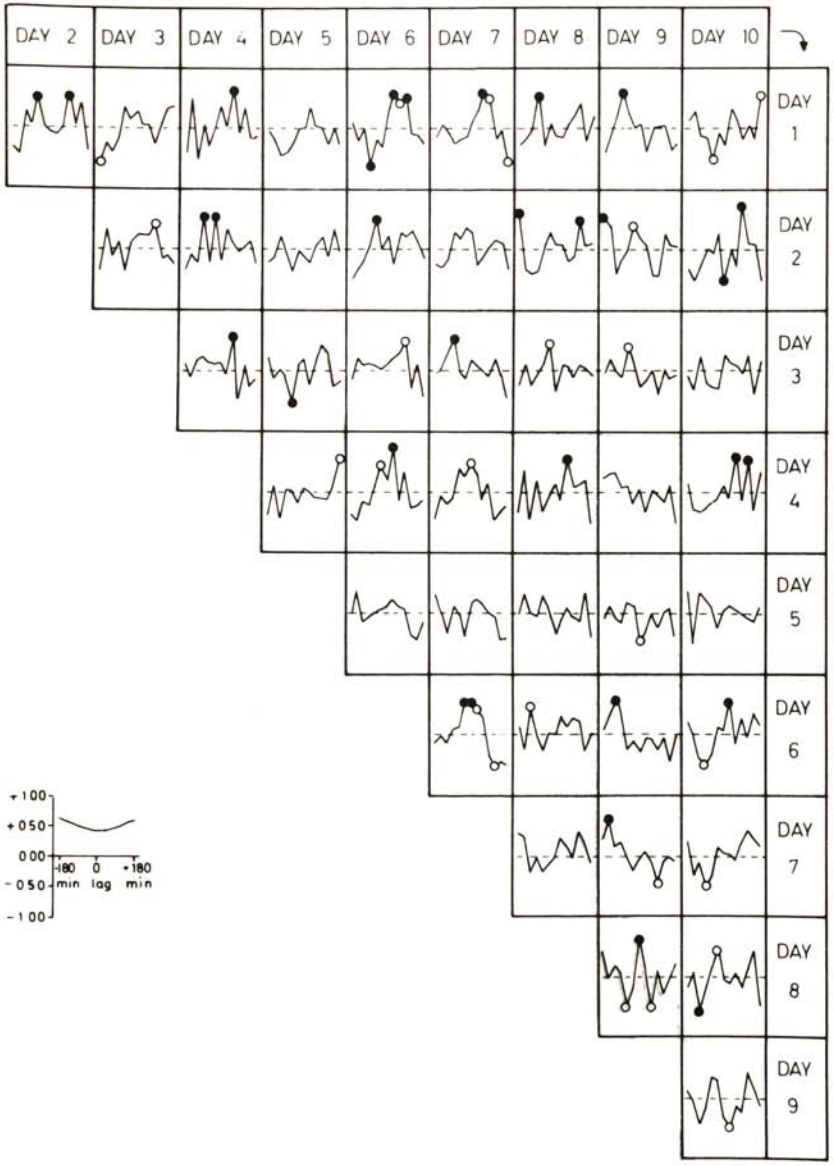

FIG. 6. CROSS-CORRELATION FUNCTIONS FOR SEXUAL BEHAVIOURS COMPUTED FOR EACH DIFFERENT PAIR OF OBSERVATION DAYS AFTER DESAUTOCORRELATION OF THE SERIES. See also Fig. 4 for other comments.

behaviours on day 1 with sexual behaviours on day 2. These symmetrical correlograms indicate that the relationship between the 2 series of observations are equivalent as would be expected if the

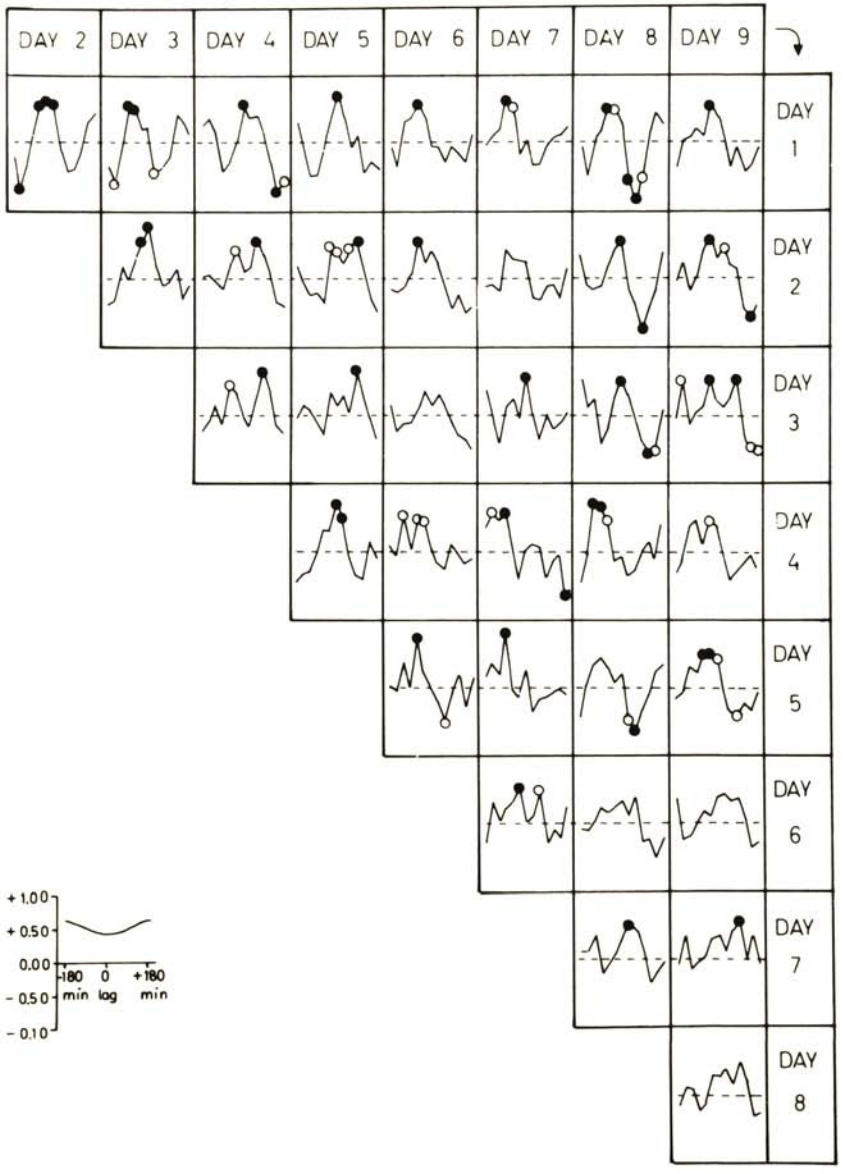

FIG. 7. CROSS-CORRELATION FUNCTION FOR THE NUMBER OF MALES IN THE POND COMPUTED FOR EACH DIFFERENT PAIR OF OBSERVATION DAYS AFTER DESAUTOCORRELATION OF THE SERIES. See also Fig. 4 for other comments.

2 series were strongly similar. This means for example that if one behaviour has occurred with a high frequency at a given hour a given day, and that the same behaviour is likely to occur also at high

frequencies x lags later on another day, then conversely if the behaviour occurs at high frequencies on the 2nd day it is likely to occur also at these high frequencies on the first day x lags later. This is however not the general case.

– The lag where significant correlations are onserved are very variable from one correlogram to another. No general rule can be formulated concerning the lags at which the series correlate except perhaps that those days of observation which were rather close in time (e.g. successive days) tend to correlate with other days at similar lags (e.g. days 2 and 3 correlate with days 1 at a lag of +4 for social displays; days 6 and 7 correlate with day 8 at a lag of +6 for social displays; days 6 and 7 correlate with day 9 at lags of –4 and –5).

In conclusion, this analysis suggests that there is some likeness between the daily distribution of displays and sexual behaviours respectively, on different days. These behavioural variables show similar distribution patterns on different days but with irregular and sometimes important time displacement from one day to another. I cannot however discard the possibility that the uninterpretable cross-correlograms are only due to the small quantity of the data for some days.

The analysis of the cross-correlograms relative to the numbers of males in the water provide more precise results. Most days are positively intercorrelated (28 out of a possible maximum total of 36) while only a few show negative significant correlations (8 pairs of days). This difference between positive and negative correlations is also very highly significant, thus strongly indicating that the number of males show similar variations during different days ($P < 0.001$ binomial test).

Most interesting however is the analysis of the lags at which these correlations occur. Almost all the positive correlations occur at negative lags or at a zero lag (left side of the correlograms) while most of the negative correlations occur at positive lags (right side). The correlations at the zero lags express the fact that the number of males show the same variations at the *same hours* on different days. The tendency of the positive correlations to shift toward the negative lags can find a good explanation in the fact that the observations were gathered during a rather long period from January to March. For that period the hour of sunrise changes for more than one hour and a half, changing from 8.31 a.m. on 23rd January to 6.40 p.m. on 23rd March (hours of sunrise at Uccle, Belgium). If the activity of the birds is synchronized with the hour of sunrise, then a maximum dependency between two days should be found for the correlation of observation series starting at their respective hours of sunrise and not of series starting at the same local hours. This means for example that an observation at 10.00 a.m. on 23rd January should be compared to an observation at about 8.15 a.m. on 23rd March (10h.00 – 1h.45 i.e. more or less the difference between the hours of sunrise on these two days). In other words, the time series on 23rd January should be delayed for a lag of more or less one hour and a half. In Figure 7, the observations

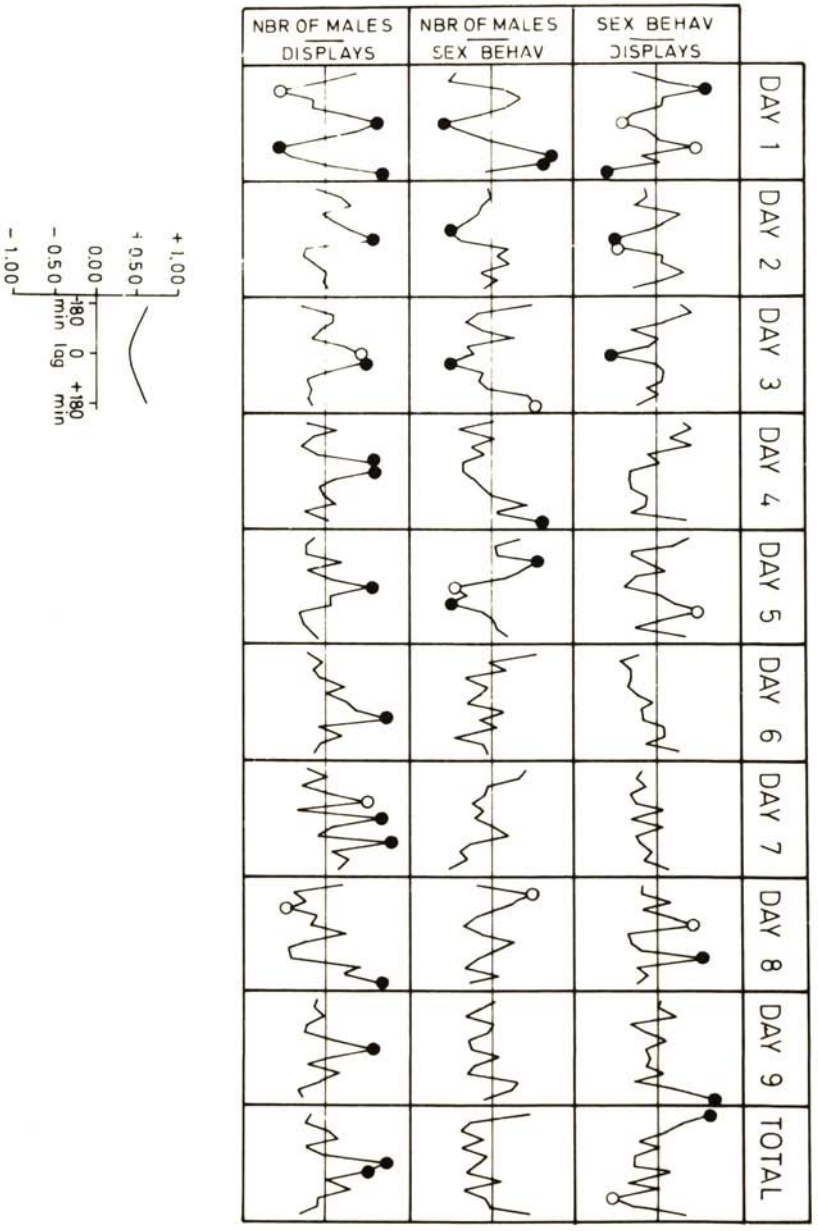

FIG. 8. CROSS-CORRELATION FUNCTIONS FOR EACH PAIR OF VARIABLES BASED ON EACH DAY OF OBSERVATION AND OH THE TOTAL OF ALL THE OBSERVATIONS. Computations have been done on the desauto-correlated series. See also Fig. 4 for other comments.

corresponding to days in the right column have been correlated with those corresponding to the days on the top line after having been delayed (negative lags, left side) or moved forward (positive lags, right side).

The clear dominance of positive correlations at negative lags expresses the fact that the series correlate better when the first series in the season is delayed relatively to the series which has been observed later in the season (e.g. when day 1 is delayed relatively to day 7) that is to say when the series are synchronized on the basis of their corresponding hour of sunrise rather than on the basis of the local time. This fact strongly supports the idea that the birds synchronize their activity on the basis of the hours of sunrise.

DEPENDENCY BETWEEN THE 3 VARIABLES STUDIED

As the last step in this study, I have also tried to find out if it was possible to observe on each day the similarity between the daily variations of the displays and the number of males and the great difference between the variations of the sexual behaviours and of the two other variables. As previously I have computed the cross-correlations between these variables on each day and for the total of all the observations using a maximum time lag of $\pm$ 6 units, i.e. $\pm$ 3 hours. The results are expressed in the form of cross-correlograms in Figure 8. In most cases I can answer affirmatively to the starting question. Only correlations occurring close to the zero lag will be discussed in detail as only data of the same day are correlated and consequently there is no reason to expect high correlations between the shifted series. There is a significant positive correlation at a zero ($\pm$ 1) lag in 7 days out of 9 between the number of males and the social displays. The totals of these 2 variables are also positively correlated at the zero lag. The expected negative correlations between the sexual behaviour and the displays on one side and between the sexual behaviours and the numbers of males on the other side, occurs frequently at lags near to zero. These correlations are especially frequent in the first days where the data are in large quantity while the correlations are more rare for the last days, this probably being explained by the fact that on these days the observations were more scarce (see section Seasonal variations). This analysis thus confirms the idea that the daily variations described in section 2 of this paper can be found on each day individually.

DISCUSSION

In this paper I have demonstrated that there are important variations of the social displays, the sexual behaviours and the number of males observed in a pond in relation with the hour of the day and with the season of observation. I want to stress however the fact that the

described variations are related "to what happens on a given pond" which defines in fact the sample which is observed (see Methods). If a relation must be set between the general activity observed on the pond and the activity of a given group of birds or even of a single bird, further assumptions must be made. One must for example assume that each bird in the observed population will display the same variations of activity as the whole group and that the number of birds which live around the pond does not systematically change as would happen if for example the birds were coming to display in the early morning on the observed pond and going to display somewhere else at noon. At this stage however these assumptions seem to be realistic and can be temporarily accepted until studies on individually-marked birds will have improved their validity.

In this study, it has also been shown that for the birds under observation, the social displays and sexual behaviours related to copulation show different temporal variations. Classically, social display is believed to promote pair formation (Heinroth 1910; Weidmann and Darley, 1971). The discrepancy in the daily and seasonal variations of social displays and sexual behaviours is however an evident objection to the classical view if the hypothesis that pair formation is reflected by an increase of the sexual behaviour can be accepted. The discrepancy of social display and pair formation in the annual course has already been discussed by Lebret (1961). It has been confirmed here quantitatively (at least if sexual movements can be taken as signs of pair formation). It must however be remembered that the variations observed are related to a group of mallards and not to individual birds. I cannot therefore ascertain at the present stage that each bird shows the described variations of behaviours though it is probable. Nevertheless the observed difference in the daily and seasonal variations of social displays and sexual behaviours raises again the disputed question of the function of social displays. I could not however conclude from these differences that the social displays do not relate to copulation as there could be subtle links which are not revealed by simultaneity of occurrence or short-term sequential organization.

Further confirmation of the unexpected daily distribution of copulation and sexual behaviours should be obtained. Weidmann (1956) has studied the activity of one pair of mallards on a single day. For that day, 2 copulations occurred at 12.30 p.m. and 3.00 p.m. this being in good agreement with our observations. A hypothesis which could explain the distribution I observed is that in the large population studied the copulations are prevented in the morning by the aggressive interactions between the males. Copulation would consequently take place in a period when birds in the water are less numerous, i.e. around noon. This hypothesis fits in relatively well with qualitative impressions collected during the observations and is worth testing further.

I would also like to mention the great similarity of the variations in social displays and the number of males on the pond. Not only do the mean values of these two variables show the same daily variations

but the cross-correlations also demonstrate that on almost each day the 2 variables are positively correlated and thus show the same pattern. This has already been felt by Tamisier (1972) who has grouped these activities in his study of the daily rhythms of the green-winged Teal (*Anas c. crecca*) and who talks of swimming including displays (nage, parades nuptiales et phases d'excitation collective). I must also mention that during the day he observed swimming in the teals at the same periods as those at which I observed peaks for social displays and number of males in the water. However most of the swimming teals were observed by Tamisier during night. It is unfortunately impossible to know if most of the displays were also observed during the night or if the nightly occurrences of swimming refer to swimming behaviour *sensu stricto*, as no distinct data are given for the displays. Anyway it is interesting to note the two close species of *Anas* reveal the same pattern of activity for similar behaviours although they have been observed by rather different methods in different places (for the period from 8.00 a.m. till 6 p.m. at least).

I shall finally discuss the interest of the auto- and cross-correlations in this study. The auto-correlation functions have not revealed at the level of the pond the short-term rhythm of activity that has been described by Raitasuo for individuals observed separately. The possible origins of this failure have already been discussed. On the other hand, the cross-correlations have shown and confirmed many interesting points among which the most interesting are the similarity in the variation of the number of males on different days, the indication of an effect of the hours of sunrise on these daily variations and the relationships between the social displays and the number of males. The method has clearly proved to be a very useful tool for the study of behavioural problems although the data were not especially well suited for these computations, since the time units were too large.

The use of filtered series has allowed the restriction of the meaning of the correlations observed and the formulation of methodological remarks. A significant correlation between two series having internal dependencies (e.g. series which show significant auto-correlations) can reflect only the internal dependency and not a link between the two series. This fact is indeed a case where, for mathematical reasons, correlation does not mean relationship. It should be related to the cases in ethology where correlation between two behaviours does not mean causal or functional relationships.

APPENDIX A

NON-PARAMETRICAL ANALYSIS

It is worth mentioning briefly here that non-parametric methods of analysis allow the same conclusions as the analysis of variance. This analysis has been undertaken with a view to providing conclusions independent of various assertions relative namely to the

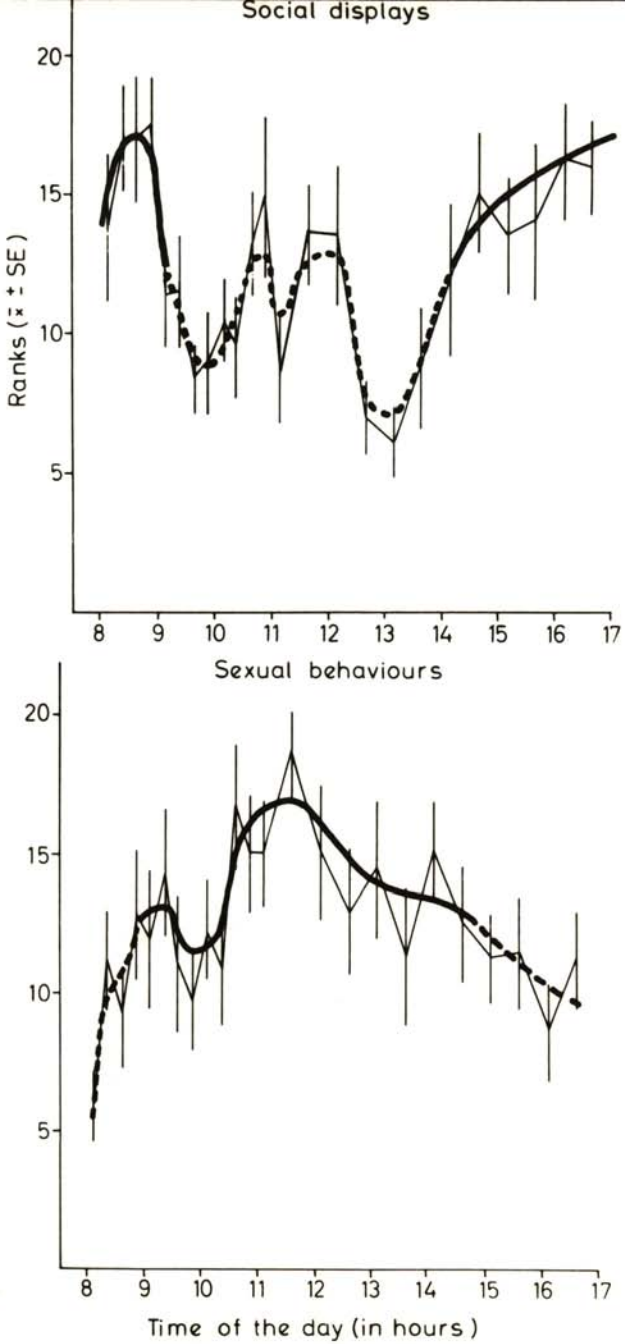

FIG. 9. DAILY VARIATION OF THE SOCIAL DISPLAYS AND SEXUAL BEHAVIOURS AS OBSERVED BY A NON-PARAMETRICAL ANALYSIS. Mean $\pm$ 1 SE of the ranks of the values are given at the different hours of observations (see text). The dotted portions of the curve are significantly lower than the parts in continuous line.

distribution of the data and which are almost impossible to check in this practical case. The frequences of sexual behaviour and social displays at the different hours have been ranked for each day in increasing order, these ranks being considered as the data for the following treatment. For each period of observation (each hour of the day) mean and standard error of the ranks have been computed and these values are plotted in the Figure 9. The "most simple curve" (which is anyway interpretative) has also been drawn passing as close as possible to most means while never getting out of the standard errors. Then using a Wilcoxon matched-pairs signed-ranks test (Siegel 1956) different portions of the curve have been compared to find out which are significantly different. As shown in Fig. 9, the only differences that can be found are that the social displays are significantly more frequent in the morning and in the afternoon while sexual behaviours occur more frequently around noon ($P < 0.01$). These were precisely the conclusions of the variance analysis.

APPENDIX B

THE FILTRATION OF AUTO-CORRELATED SERIES

I think it is necessary to explain briefly here why cross-correlations have been computed on filtered series and why this improves the meaning of the significant cross-correlations obtained. Let us suppose that we have 2 time-series auto-correlated at the kth order

$$x_1(t) = \alpha_1^k \, x_1(t-k) + \varepsilon_1(t)$$

$$x_2(t) = \alpha_2^k \, x_2(t-k) + \varepsilon_2(t)$$

in which $\varepsilon_1(t)$ and $\varepsilon_2(t)$ are white noises ($\bar{\varepsilon}_i = 0$) and α_i^k are the auto-regression coefficients of the series. If x_1 and x_2 are not cross-correlated then their cross-covariance will be null for any time lag (u) between the 2 series

$$\gamma x_1 x_2(u) = 0$$

As we do not consider the whole series but only samples of them, their cross-covariance is only known through an estimator $cx_1x_2(u)$ affected itself by a variance. It can be shown in our case that the variance of the covariance estimator is expressed in the form

$$\text{Var. } [cx_1x_2(u)] \approx \frac{\sigma_1^2 \cdot \sigma_2^2}{N} \cdot \frac{1+\alpha_1\alpha_2}{1-\alpha_1\alpha_2}$$

in which σ_1^2 and σ_2^2 are the variances of the series and $\alpha_1\alpha_2$ their auto-regression coefficients (cfr. Jenkins and Watts, 1968, pp. 336-340).Thus if x_1 and x_2 are white noises (i.e. if α_1 and $\alpha_2 = 0$)

$$\text{Var } [cx_1x_2(u)] \approx \frac{\sigma_1^2 \quad \sigma_2^2}{N}.$$

Hence if $\alpha_1\alpha_2$ is positive (i.e. if the *2* series are positively or negatively auto-correlated) the variance of their cross-covariance estimator is inflated relative to the case of 2 white noises (for in this case $\frac{1+\alpha_1\alpha_2}{1-\alpha_1\alpha_2}$ is greater than 1). Whereas if $\alpha_1\alpha_2$ is negative (in the case where one series is positively auto-correlated and the other is negatively) the variance is deflated. However it is generally the case that the 2 series are auto-correlated both positively or both negatively so that $\alpha_1\alpha_2$ is positive.

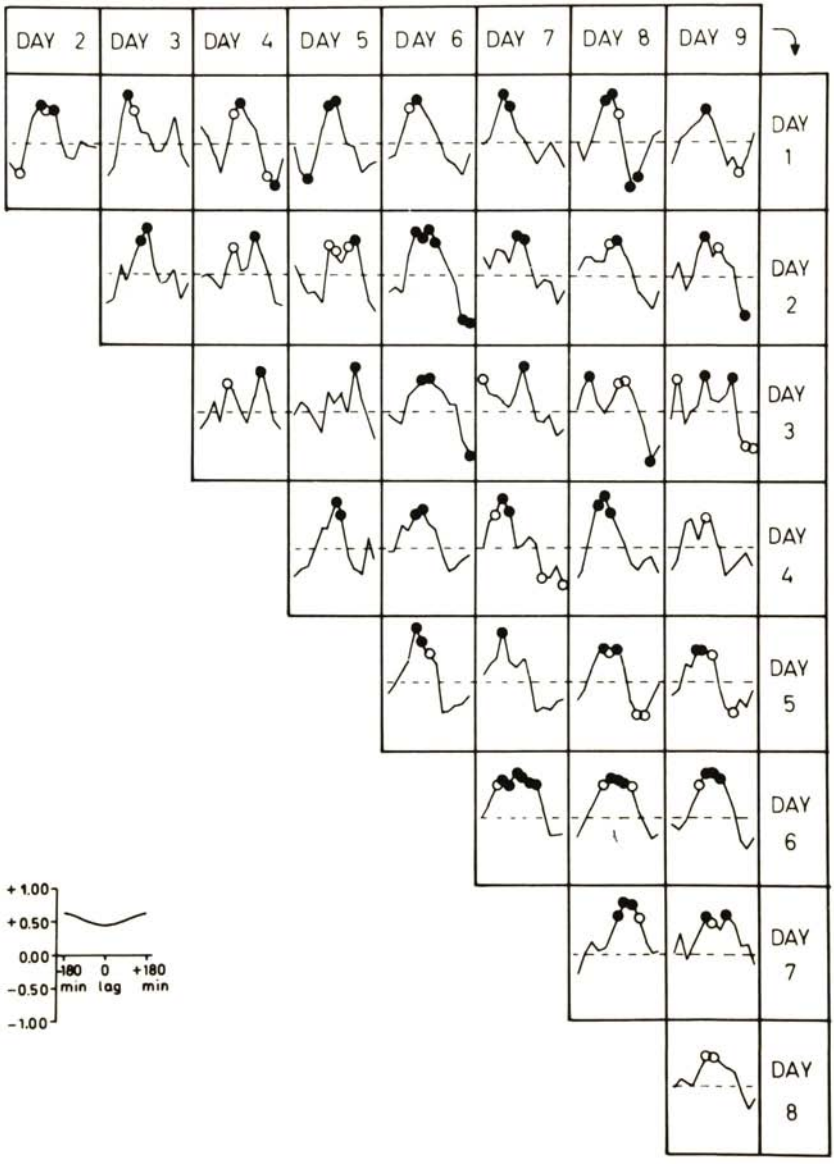

FIG. 10. CROSS-CORRELATION FUNCTIONS FOR THE NUMBER OF MALES IN THE POND COMPUTED FOR EACH DIFFERENT PAIR OF OBSERVATION DAYS WITHOUT DESAUTO-CORRELATION OF THE SERIES (see text). See also Fig. 4 for other comments.

This means that generally the variance of the cross-covariance estimator is greater for auto-correlated series than for white noises. This increases the probability of finding significant cross-correlation coefficients between auto-correlated series which are however

not cross-correlated. Very large cross-covariances, all of them spurious, can be generated between two uncorrelated processes as a result of large auto-covariances within the two processes.

If a test is required for correlation between two time series which are auto-correlated, a filtering operation should be carried out on the two series to covert them into white noise before computing the cross-covariance function. The α coefficients have to be computed and then the 2 series x_1 and x_2 are filtered to obtain desauto-correlated series x_1' and x_2' so that

$$x_1'(t) = x_1(t) - \alpha_1^k x_1(t\text{-}k) = \varepsilon_1(t)$$

$$x_2'(t) = x_2(t) - \alpha_2^k x_2(t\text{-}k) = \varepsilon_2(t)$$

This should be done theoretically for any time lag k where significant auto-correlation is observed. However as the observed series are relatively small in my case, filtering has only been carried out for auto-correlation at a lag of $\pm$ 1. This computation procedure has been used in all the auto-correlations presented here. In some cases however, cross-correlations have been computed comparatively with filtered and non-filtered series so as to improve the validity of the procedure. As an example, comparative cross-correlograms for the number of males computed between each different pairs of days will be presented.

Results in Fig. 10 were obtained with non-filtered series and can be compared with results in Fig. 8 where desauto-correlation was performed. As can be observed the number of significant correlation coefficients is much higher in the case of non-filtered series. For $P \leqslant 0.05$, 74 coefficients are significant in Fig. 10, while only 45 are in Fig. 8. It can further be observed that the cross-correlograms which are the most affected by the use of a filter are those computed between strongly auto-correlated series (see Fig. 5 for the auto-correlograms). For example, it can be observed in Fig. 5 that the number of males is significantly auto-correlated on day 6 and day 7. If the cross-correlograms between these 2 series are computed with and without a filter greater differences effectively occur. Without a filter, the 2 series are significantly correlated for almost any lag (Fig. 10) but after filtration only one significant correlation coefficient is retained at a lag of minus one.

Most of the correlograms in Fig. 8 retain anyway one or two significant correlation coefficients generally near the zero lag. Further, the remaining coefficients are easier to interpret than the numerous ones which were obtained on non-filtered data. The filtering procedure seems thus to be well adapted to the problem encountered as it retains generally only those coefficients which have a clear ethological interpretation and as it gives to these coefficients a more restricted meaning. This is because they are affected by smaller variances, consequently there is a smaller probability that they are significant only by chance.

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