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Patterns of interaction in the courtship behaviour of shags (*Phalacrocorax aristotelis*)

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ABSTRACT. *Patterns of interaction in the courtship behaviour of shags* (Phalacrocorax aristotelis).- A quantitative analysis was made of 448 courtship sequences that included 3346 separate events. Of the 272 possible transitions only 36 reached significance. The analysis revealed two clearly differentiated groups of behaviours with only one significant transition between groups. One group included behaviours leading to copulation. The other consisted of behaviours that indicate a readiness to mate, and included the male advertising displays and other behaviours of the male which direct the bill away from the female, as well as the approach and mount by the female. The function of this second group of behaviours appears to be to advertise readiness to form a pair.

KEY WORDS. Shag, *Phalacrocorax aristotelis*, Courtship, Interactions, Sequential analysis

Introduction

A central interest of classical ethology was in the descriptions of the sequences of species specific behaviour, especially courtship behaviour. For some time now, patterns of courtship have received scant attention in the literature, but research in other areas has given new relevance to their study. In behavioural endocrinology the reproductive behaviour of Barbary doves (*Streptopelia risoria*) shows a correlation between sequences of transitions in behaviour and hormonal levels: the transition from aggressive courtship to nest-oriented courtship is related to the androgen levels (Hutchison & Katongole, 1975; see Hutchison & Hutchison, 1983 for a review). The changes in the sequences of behaviour that are displayed during such a transition are complex and require description. Another area where detailed analysis of the sequences of behaviours is important is in studies of differences in reproductive strategy within a population. Extra-pair copulations do result in paternity in some species (Alatalo et al., 1984; Møller, 198 ; Westneat, 1987 a,b), but only by examining the females' sequences of behaviours can soliciting be distinguised from acceptance or even being forced. Moreover, the discrepancy between observed extra-pair copulation rates and extra-pair paternity in some species may be due to differences in the timing of

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extra-pair copulations or to differences in the sequences of behaviours involved (Birkhead, 1987).

The courtship of different species of *Phalacrocorax* was studied by several workers: the behaviours that make up the courtship of the shag, *Phalacrocorax aristotelis*, were carefully categorised and described by Snow (1963), and for the cormorant, *P. carbo*, by Kortlandt (1940). The social communication behaviours of seven species of *Phalacocorax* were discussed by van Tets (1965) who did a comparitive study of the Pelecaniformes looking at the functions and phylogeny of the social communication behaviours of 15 species in the order.

In addition to describing the postures and movements that make up each category of behaviour, Snow and Kortlandt gave qualitative descriptions of short sequences of courtship behaviour. However, to date no quantitative study has been done of the sequences of behaviours used in courtship for any of the Phalacrocoracidae.

The first step in examining the sequence of behaviours is to look at the transitions from each behaviour to all others. The resulting matrix of frequencies can be used to draw flow diagrams without any statistical considerations, or it can be compared with a random model in order to avoid the problem of spurious patterns resulting from common behaviours (Slater, 1983).

Recently a number of methods for comparing ·equencies of transitions between behaviours with various models have become available. We used ELAG, a program developed by Bakeman (1983), to calculate the probability and significance of a behaviour of one animal following a particular behaviour of another animal in diadic interactions.

Methods

The observations were collected in 1984 from individually colour ringed shags breeding on a focal area of the Isle of May, Scotland (56° 11' N 2° 33' W). Data were collected from 51 shags, 24 males and 27 females. These eventually formed 22 laying pairs. Eleven of the males were observed displaying to more than one female, six to more than two.

Observations were made from a permanent hide overlooking the subcolony across a 6m wide inlet that was uncovered only at low tide. The focal nests were between 11 and 15 m from the hide. Observations were made for 147 hours spread over one week in late March, one week in mid April, 5 days in early May, 10 days in mid May and 6 days in June (from early courtship to laying). Except in March, when the shags were seldom present on the colony, six hours of observations were made daily: two hours from first light or 05.30 BST, whichever came later, one hour at 12.00 and three hours from 16.00. In any one day simultaneous focal observations were made on four territories. When a courtship sequence started on one of these, each behaviuor and time was recorded on a portable computer. If a sequence started on one of the other territories a note was made on a tape recorder of when and which bird was involved while continuing to record the sequence on the first territory. The behaviours were recorded as each bird began a particular behavioural category. Thus if a male dart gaped at a female, then threw back, and the female began to approach and the male gave a sitting bow as she reached him, this was recorded as Dart Gape, Throw Back, Female Approach, and Male Sitting Bow. A bout of behaviour was considered over and recording was stopped if either of the partners left the area or if the pair ceased interacting for more than 1 minute.

Behavioural Categories

The following categories, adapted from Cramp & Simmons (1977), Snow (1963) and van Tets (1965) were used: Dart Gape (DG, males only), Throw Back (TB, males only),Sitting Bow (both sexes, MSB and FSB; in the following descriptions M or F as a first letter indicates sex), Standing Bow (both sexes, MStB and FStB), Up Gape (both sexes, MUP and FUP), Throat Click (both sexes, MTC and FTC), Mount (both sexes, MM and FM), Copulation (Co), Male Approach (MA), Female Approach (FA), and Driven Away (DA). We used Stop (ST) to record any termination of a sequence of pair behaviours, either when one of the pair moved away or went to a non-pair behaviour, e.g. self preening, or when the pair ceased interacting for more than 5 seconds.

The male behaviours Dart Gape, Throw Back and Bow are termed advertising displays in the literature (Snow, 1963; van Tets, 1965; Cramp & Simmons, 1977).

There are other affiliative behaviours in the shag, allopreening and quivering nest material, which were not used in this analysis. Extensive allopreening could occur at any stage after the pair bond was formed, but seemed to be most common after the eggs had been laid. Quivering nest material and approaching holding out nest material to be quivered were found to be quite important in diverting the aggression of the male (van Tets, 1965). Unfortunately, this was not appreciated in time to include it in the data gathering process.

Analysis

Coding of behaviours

For analysis the behaviours were coded as events disregarding their duration (Martin & Bateson, 1986). If a behaviour was followed by the same behaviour this was coded as a single occurrence to avoid autotransitions. If autotransitions are not excluded then the diagonal will contain inflated frequencies unless the divisions between bouts of the same behaviour are clear (Slater, 1973). Bouts of behaviours with a separation of more than 5 seconds between them or with another behaviour of the other bird intercalated were coded as distinct events separated by stop or the other event.

Sequential analysis

Sequential analysis was carried out using the ELAG program of Bakeman (1983). ELAG reads the sequences of behaviours and calculates the frequency of the transitions from each behaviour to all others. It also calculates a binomial z-score for each transition comparing the observed probability with the expected first-order random model, using a formula by Sackett (1979). (Alternatively, ELAG also allows a less conservative calculation of the z-score using the formula of Allison & Liker (1982).)

Our analysis is similar to the more traditional method obtained by collapsing the total matrix of transitions into a 2x2 matrix for each cell and computing the χ^2 score (Slater, 1983), since the z^2 is equal to the χ^2 value obtained in this way (Fienberg, 1980).

Criteria for significance

In order for a transition to be significant we used two criteria: that the z-score had to be >1.96 corresponding to $p<0.05$ and an arbitrary decision that the transition had to occur more than 5 times.

There are two problems associated with sequential analysis: the number of events and the independence of the cells. In addition to these, in our analysis we have pooled over individuals (Machlis et al. 1985). Fagen & Young (1978) recommend that sequential analysis only be attempted when there are $10r^2$ transitions, where r is the number of behavioural categories used. Thus for the 17 categories we used, we required more than 2890 transitions. Only by pooling over individuals could we have 3346 transitions.

The second problem is more difficult since in a sequential analysis subsequent transitions share a

TABLE I. Matrix of transitions from courtship behaviours (see text).
[Matriz de transiciones de las conductas de cortejo (Vease el texto).]

		FOLLOWS																
		MA	MTC	MM	FUP	FSB	Co	FStB	FTC	DG	TB	FA	FM	MUP	MSB	MStB	DA	ST	Totals
	MA		7	0	43	0	0	0	0	0	0	0	0	3	0	0	0	0	53
	MTC	1		73	134	5	0	5	4	0	0	1	0	28	2	2	0	91	346
	MM	0	6		139	22	9	1	0	0	0	0	0	4	0	2	0	21	204
	FUP	0	134	80		168	3	13	3	0	0	0	3	37	1	11	1	216	670
	FSB	0	6	17	34		85	0	0	0	0	0	0	1	0	0	0	60	203
P	Co	0	2	0	20	2		0	0	0	0	0	0	10	1	0	0	76	111
R	FStB	0	3	4	3	1	0		0	0	0	0	0	0	0	0	0	11	22
E	FTC	0	2	4	2	0	0	0		0	0	0	2	0	0	0	0	9	19
C	DG	0	0	0	0	0	0	0	0		93	5	0	1	0	0	0	30	129
E	TB	0	0	0	0	0	0	0	0	38		30	0	2	4	1	2	25	102
E	FA	0	0	0	1	0	0	0	0	9	2		3	46	12	4	2	12	91
D	FM	0	0	0	1	1	0	0	0	0	0	0		48	9	0	1	5	65
S	MUP	0	28	9	56	1	1	1	3	0	3	7	12		186	78	0	108	493
	MSB	0	1	1	5	0	14	0	0	0	0	3	26	81		1	1	106	239
	MStB	0	2	0	2	0	0	1	2	1	0	0	10	25	0		1	88	132
	DA	0	0	0	0	0	0	0	0	4	1	0	0	0	1	1		8	15
	ST	4	61	12	149	3	0	1	4	27	3	2	6	114	26	26	14		452
	Totals	5	252	200	589	203	112	22	16	79	102	48	62	400	242	126	22	866	3346

common element with the preceding transition. However, Bakeman & Dorval (in press) have used a Monte Carlo method with random data and concluded that this apparent violation of sampling independence in sequential analysis does not affect the results of the analysis.

Results

A total of 448 sequences of behaviours were recorded with 3346 behavioural events. The mean length of the chains of behaviours was 7.47 events. Table I presents the matrix of observed transitions from one behaviour to another. Of the 272 possible transitions only 36 reached criterion, of these 7 have p values <0.05, 3 <0.01, 2 <0.001 and 24 <0.00001. The diagonal is empty since autotransitions were excluded in the recording.

Figure 1 illustrates the sequence diagrams for the significant transitions in the data. Inspection of the figure shows that the transitions fall into two sets. With one exception all significant transitions are within the categories shown above the Stop category or within those shown below it. The only transition between these two sets of categories is from Male Sitting Bow to Copulation. Stop is the only category included in both sets.

The first group (upper half, fig. 1) is composed of the set of behaviours Male Approach, Female Up Gape, Male Throat Click, Female Standing Bow, Female Sitting Bow, Copulation and Stop. The second group (lower half, fig. 1) consists of the set Female Approach, Dart Gape, Throw Back, Female Throat Click, Male Up Gape, Male Standing Bow, Male Sitting Bow, Female Mount, Driven Away and Stop.

Table II presents typical sequences of both sets of behaviours. The sequences in the first set begin

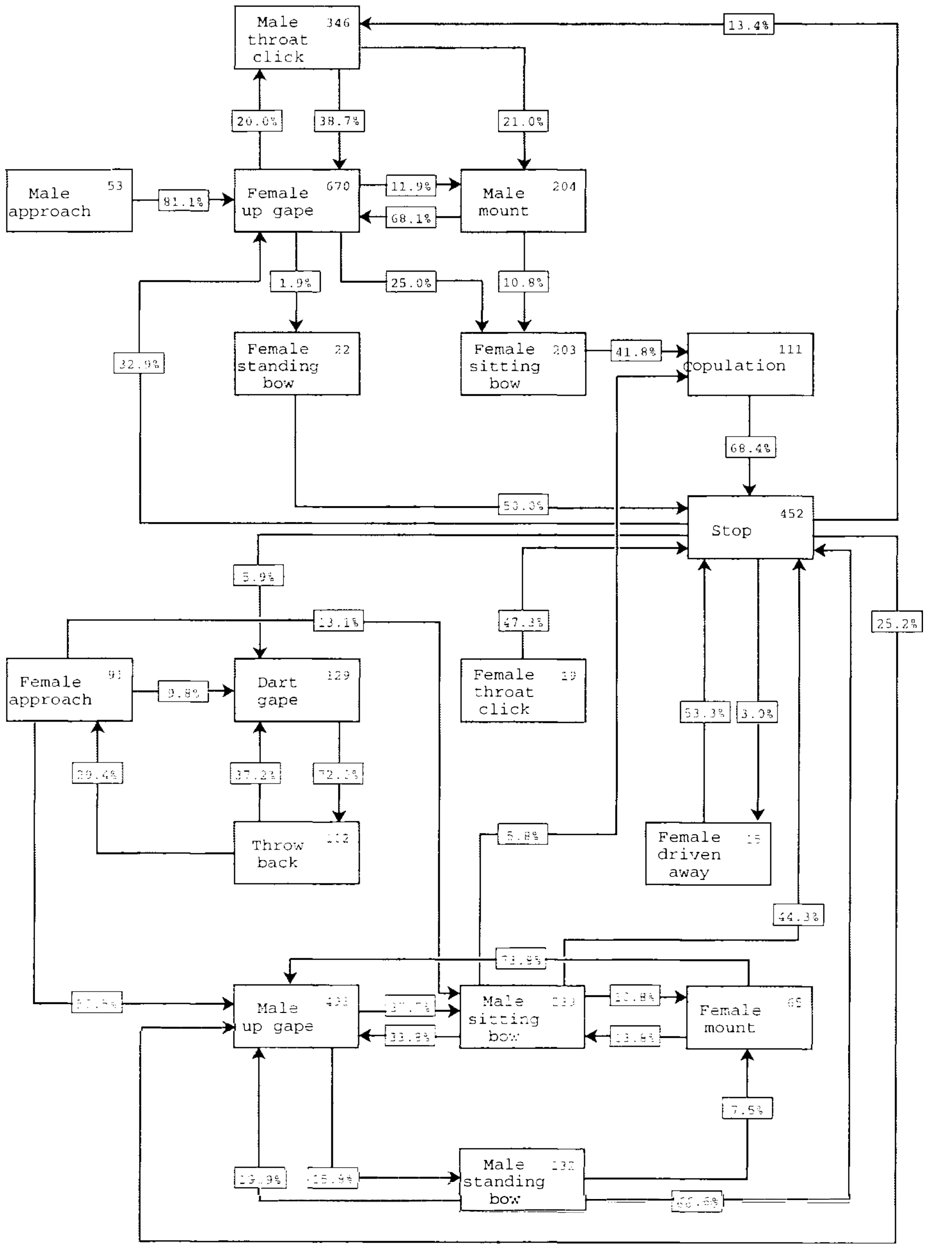

FIGURE 1. Significant transitions of the courtship behaviours.
[Transiciones significativas de las conductas de cortejo.]

TABLE II. An example of sequences of shag courtship.
[Ejemplo de secuencias de cortejo en el cormoran moñudo.]

GROUP 1	
	FUG-MTC-FUG-MTC-FUG-MM-FUG-FSB-FUG-FSB-Co-ST-FUG-ST
	MTC-MM-FUG-FSB-Co-FUG-ST-FUG-ST
	MTC-FUG-ST-MTC-FUG-ST-FUG-MTC-FUG-MM-FUG-FSB-Co-ST-FUG-ST
	MM-FUG-FSB-Co-ST
	FUG-ST-FUG-ST-MTC-FUG-MM-FUG-FSB-Co-ST-FUG-ST-FUG-ST
GROUP 2	
	FM-MUG-MSB-MUG-MSB-ST
	DG-TB-FA-MUG-FUG-MSB-ST-MSB-MUG-MSB-MUG-MSB-ST
	DG-TB-DG-TB-FA-MSB-ST-MSB-ST
	DG-TB-DG-TB-FA-MSB-MUG-MSB-MUG-MSB-MUG-MSB-MUG-MSB-MUG-ST

with Male Approach followed by Female Up Gape. These sequences show a common cycle of behaviours with Male Throat Click followed by Female Up Gape followed by Male Throat Click again and another cycle of Female Up Gape followed by Male Mount followed by Female Up Gape. These cycles are indicated in figure 1 by the bidirectional arrows. In almost half the cases when the sequence gets to Female Sitting Bow it goes on to Copulation.

The sequences in the second set typically begin with either Female Approach or with Dart Gape followed by Throw Back. As the bidirectional arrows indicate the cycle of Dart Gape to Throw Back to Dart Dape is very common and may be repeated a number of times continuing until the female reaches the male. Once the female reaches the male or mounts him, Male Sitting Bow follows and cycles with Male Up Gape. Most sequences end at this point with Stop or Driven Away. In a few cases there is a transition from Male Sitting Bow to Copulation.

Discussion

The analysis revealed two clearly established patterns, one which led to Copulation (group 1, upper half of fig. 1) and a second (group 2, lower half of fig. 1) which did so only rarely. While some of the possible transitions between behaviours of different groups did occur, only the transition from Male Sitting Bow to Copulation was significant at the 0.05 level.

A male will use the male behaviours in group 1 only with a female he is already paired with in that he freely accepts her onto the territory without attacking her as she approaches and is allowed to stay on the territory when he returns. A female will use the female behaviours such as Female Up Gape and Standing or Sitting Bow only towards a male who has already accepted her.

The group 2 behaviours are used in a different context, that of a male and female who are not yet paired and the female runs considerable risk of being attacked in attempting to enter the territory. This group includes the Male Dart Gape and Throw Back which have been termed male advertising displays (Snow, 1963; van Tets, 1965; Cramp & Simmons, 1977). These behaviours show features for detection at a distance or over noise (Wiley, 1983): they are extremely conspicuous both in the amplitude of the movements and in their repetitiveness. Armstrong (1947) and Fisher & Lockley (1954) described them as violent, and they are the only courtship displays of the shag that are singled out for description by Whitherby et al. (1940). Since the male and female are frequently actually in physical contact during the Throw Back, any noise that the displays are designed to overcome can only come from the competing displays of other males in the colony and not the need to be detected at a distance. The other behaviours in group 2 include the Male Up Gape and Bows and the Female Mount. Snow (1960) pointed out that it is important for a strange female to avoid having the male point his bill directly at her or her bill at him. When this does happen the male attacks. The male Throw Back, Sitting Bow and Up Gape and Sitting Bow sequence, which is common early in the relationship, carefully keeps the male's beak pointing either at the ground or straight up and away from the female. A female who comes to a strange male sometimes sits on his back in the Female Mount behaviour while he is in the Sitting Bow position. From here she pokes at the nest site and carefully keeps her head away from the male's whenever he raises his head from the Sitting Bow position. Male Sitting Bow behaviour is the one exception to the lack of significant transitions between groups. This exception could be due to the use of Female Mounts, the behaviour that preceeds it, in different contexts. But up to this time only a few studies (Nuechterlein & Storer, 1989 : Bowen et al., 1991; Ortega Ruano & Graves, 1991) have tried to disentangle the possible functions of Female Mount, or reverse mountings as they are usually called, and further studies will be required.

When a set of behaviours can be broken down into two or more subgroups where all or nearly all the transitions are within and not between the subgroups then the set is said to be nearly decomposible (Simon, 1981). The courtship of the Shag is such a system. Dawkins (1976) has argued that this property indicates that the clustering of sequences of behaviour observed represents more than temporal clustering. A lack of significant transitions would indicate that the two subsets are under separate hierarchical control; they are organised into separate hierarchies of decisions and used in different, non-overlapping contexts or have separate functions. In the case of the courtship of the shag, the behaviours in group 1 are the courtship behaviours that lead to copulation, those in group 2 are used to attract a strange female to the territory.

Resumen

Patrones de interacción en la conducta de cortejo del cormoran moñudo (Phalacrocorax aristotelis).

Se estudió el cortejo de 51 cormoranes moñudos, 24 machos y 27 hembras de una colonia de la isla de May, en Escocia (56º 11' N 2º 33' W). Se registraron 448 secuencias de cortejo con un total de 3346 eventos, y se analizaron las transiciones entre los distintos eventos (tabla I), utilizando un programa de análisis secuencial, ELAG. De las 272 transiciones, solo 36 resultaron estadísticamente significativas (fig. 1). Las conductas de cortejo podían separarse en dos grupos claramente diferenciados: todas las transiciones significativas, salvo una, se daban entre conductas pertenecientes al mismo grupo. El primer grupo (mitad superior de la fig. 1) comprendía tres conductas del macho, Aproximación (MA), Clic (MTC) y Monta (MM), y otras tres de la hembra, Pico abierto hacia arriba (FUG), Arco agachado (FSB) y Arco de pie (FStB). Estas seis conductas finalizaban en la cópula (Co). Las secuencias con conductas del primer grupo mostraban un alto grado de repetición (tabla II). El segundo grupo (mitad inferior de la fig. 1) estaba formado por seis conductas del macho, Dardo (DG), Garganta hacia atras (TB), Pico abierto hacia arriba (MUG), Arco agachado (MSB), Arco de pie (MStB) y Expulsión de la hembra (DA), y por tres conductas de la hembra, Aproximación (FA), Clic (FTC) y

Monta (FM). Las secuencias típicas de este segundo grupo mostraban un alto grado de repetición de las conductas iniciales (vease tabla II).

Los dos grupos de conductas tienen funciones totalmente diferentes, el primero está formado por las conductas de cortejo que conducen a la copulación y el segundo tiene por objetivo la atracción de una hembra al territorio y la formación de pareja.

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References

Alatalo, R.V., Gottlander. K. & Lundeberg, A., 1987. Extra-pair copulations and mate guarding in the polyterritorial Pied Flycatcher (*Ficedula hypoleuca*). *Behaviour*, 101:139-155.

Armstrong, E.A., 1947. *Bird Display and Behaviour*: *An Introduction to the Study of Bird Psychology*. London: Lindsay Drummond.

Bakeman, R., 1983. Computing lag sequential statistics: the ELAG program. *Behav. Res. Methods & Inst*. 15:530-535.

Bakeman, R, & Dorval, B., (in press) The distinction between sampling independence and empirical independence in sequential analysis. *Behav. Assessment*.

Birkhead, T.R., 1987 Sperm competition in birds. *Trends Ecol. Evolut*., 2:268-272.

Bowen, B.S.; Koford, R.R. & Vehrencamp, S.L., 1991. Seasonal pattern of reverse mounting in the Groove-billed Ani (*Crotophaga sulcirostris*). *Condor*, 93:159-163.

Cramp, S. & Simmons, K.E.L., 1977. *Handbook of the birds of Europe, the Middle East and North Africa*, Vol I. Oxford: Oxford University Press.

Dawkins, R., 1976. Hierarchical organisation: a candidate principle for ethology. In: *Growing Points in Ethology*:7-54 (P.P.G. Bateson & R.A. Hinde, Eds), Cambridge: Cambridge University Press.

Fagen, R.M. & Young, D.Y., 1978. Temporal patterns of behaviour: durations, intervals, latencies and sequences. In: *Quantitative Ethology*: 79-114 (P.W. Colgan, Ed.), New York: John Wiley and Sons.

Fienberg, S.E., 1980. *The analysis of cross-classified categorical data* (2nd ed.) Cambridge, Mass.: MIT Press.

Fisher J. & Lockley, R.M., 1954. *Sea-Birds*. London: Collins.

Hutchison, J.B. & Hutchison, R.E., 1983.Hormonal mechanisms in mate choice in birds. In: *Mate choice*: 389-405 (P.P.G. Bateson, Ed), Cambridge: Cambridge University Press, 1983.

Hutchison, J.B. & Katongole, C.B., 1975. Plasma testosterone in courting and incubating male Barbary doves (Streptopelia risoria). *J. Endocrin*. 65:275-276.

Kortland, A., 1940. Eine Uebersicht der angeborenen Verhaltungsweisen des Mittel-Europaeischen Kormorans *Phalacrocorax carbo sinensis* Shaw & Nodd, ihre Funktion, ontogenetische Entwicklung und phylogenetische Herkunft. *Arch. Neerl. Zool*. 4:401-442.

Machlis, L., Dodd, P.W.D. & Fentress, J.C., 1985. The pooling fallacy: problems arising when individuals contribute more than one observation to the data set. *Zeitsch. Tierpsychol.*, 68:201-214.

Martin, P. & Bateson, P.P.G., 1986. *Measuring Behaviour: An introductory guide*. Cambridge: Cambridge University Press.

Møller, A.P., 1987. Behavioural aspects of sperm competition in swallows. *Behaviour*, 100:92-104.

Nuerchterlein, G.L. & Storer, R.W., 1989. Reverse mounting in grebes. *Condor*, 91:341-346.

Ortega Ruano, J. & Graves, J.A. (1991). Reverse mounting during the courtship of the european Shag (*Phalacrocorax aristotelis*). *Condor*, 93:859-863.

Sackett, G.P., 1979. The lag sequential analysis of contingency and cyclicity in behavioral interaction research. In: *Handbook of Infant Development*: 623-649 (J.D. Osofsky, Ed.), New York: Wiley and Sons.

Simon, H.A., 1981. *The sciences of the Artificial*. (2nd Ed.) Cambridge, Mass.: M.I.T. Press.

Slater, P.J.B., 1973. Describing sequences of behaviour. In: *Perspectives in Ethology*. Vol 1.: 131-153 (P.P.G. Bateson & P.H. Klopfer, Eds.), New York: Plenum Press.

Slater P.J.B., 1983. The study of communication. In: *Animal Behaviour*. Vol 2 *Communication*: 9-42 (T.R. Halliday & P.J.B. Slater, Eds.), Oxford: Blackwell Scientific Publications.

Snow, B.K., 1963. The behaviour of the Shag. *Br. Birds*, 56:77-103, 164-186.

van Tets, G.F., 1965. A comparative study of some social communication patterns in the Pelecaniformes. *Ornithological Monographs No 2*, Amer. Ornith. Union.

Westneat, D.F., 1987a. Extra-pair copulation in a predominantly monogamous bird: observations of behaviour. *Anim. Behav.*, 35:865-876.

Westneat, D.F., 1987b. Extra-pair fertilizations in a predominantly monogamous bird: genetic evidence. *Anim. Behav.*, 35, 887-886.

Wiley, R.H., 1983. The evolution of communication: Information and manipulation. In: *Animal Behaviour* vol 2 *Communication*: 156-189 (T.R. Halliday & P.J.B. Slater, Eds.). Oxford: Blackwell Scientific Publications.

Witherby, H.F., Jourdain, F.C.R., Ticehurst, N.F. & Tucker, B. W., 1940. *The Handbook of British Birds*, vol IV. London, Witherby.

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