

# Extra-pair copulations of grey heron *Ardea cinerea* in Arcachon Bay (SW France)

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*Extra-pair copulations of grey heron Ardea cinerea in Arcachon Bay (SW France).*— In a colony of grey heron *Ardea cinerea*, located on the French Atlantic coast (Arcachon Bay), the copulatory behaviour of herons was observed during two breeding periods (1992 and 1993). A total of 181 intra-pair copulation attempts and 11 extra-pair copulation attempts (5.7% of all copulation attempts) were observed. Eighty-nine percent of the intra-pair copulation attempts and 54.5% of extra-pair copulation attempts were successful. Ten of eleven male herons involved in extra-pair copulation attempts were paired and had their nests close to the target female nests. Only one male involved in EPCAs was unmated. In two cases of extra-pair copulation attempts, the target females deserted the nest after the attempt, during their egg-laying period (the most important fertile period). All extra-pair copulations were made during the egg-laying period of the target females and during both incubation and guardian periods of the males.

Key words: *Ardea cinerea*, Breeding period, Extra-pair copulation attempts, Grey heron, Sperm competition.

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## Introduction

Some authors (TRIVERS, 1972; GLADSTONE, 1979; BIRKHEAD & MØLLER, 1992) have suggested that extra-pair copulation is part of a mixed reproductive strategy among males of most bird species considered monogamous. High pair copulation rates and mate-guarding behaviour among many colonial birds have been interpreted as two different aspects of the paternity defence in a sperm competition context (BIRKHEAD et al., 1987).

The grey heron *Ardea cinerea* is a colonial and monogamous species, in which extra-pair copulation attempts have been reported: in the Netherlands (VERWEY, 1930), France (MARION, 1979) and Spain (RAMO, 1993), but in England (MILSTEIN et al., 1970) and Belgium (VAN VESSEM & DRAULANS, 1986) no extra-pair copulation attempts were observed.

Extra-pair copulation attempts have also been reported for many colonial breeding birds (mainly Ciconiformes): white stork *Ciconia ciconia* (TORTOSA & REDONDO, 1992), spoonbill *Platalea leucorodia* (AGUILERA & ÁLVAREZ, 1989; AGUILERA, 1994), bittern *Botaurus stellaris* (VOISIN, 1991), little bittern *Ixobrychus minutus* (LANGLEY, 1983), little egret *Egretta garzetta* (VOISIN, 1976), cattle egret *Bubulcus ibis* (FUJIOKA & YAMAGISHI, 1981; MCKILLIGAN, 1990), white ibis *Eudocimus albus* (FREDERICK, 1987) and scarlet ibis *Eudocimus ruber* (RAMO & BUSTO, 1985). However, the extra-pair copulation behaviour has not always been related with an act of sperm competition (TORTOSA & REDONDO, 1992). Furthermore, extra-pair copulations do not appear to significantly affect the paternity of the brood, as they mostly occur after egg-laying (FUJIOKA & YAMAGISHI, 1981).

Extra-pair copulation behaviour involves several hazards for males (sperm depletion, parasite or disease transmission, predation and divorce) and for females (injury, disease or parasite transmission, predation and foraging hazard of nearby male) and also several benefits for males (increased fitness, insurance of mate acquisition, insurance against partner's infertility and quality of offspring) and for females (genetic diversity and quality, avoidance of infanticide, reduced sperm supplies for competing females and protection against genetic defects arising from prolonged sperm storage) (BIRKHEAD & MØLLER, 1992), and the two sexes have to discrimi-

nate the profits and losses of this reproductive strategy.

The aim of this paper was to show the distribution of intra- and extra-pair copulation attempts during both breeding and diurnal cycles, taking into account the presumed fertile period of the female herons.

## Study area and methods

The study was conducted in a mixed-species heronry located in the Ornithological Park of Le Teich (Arcachon Bay, Atlantic coast of France), during two breeding periods (1992 and 1993). At this colony four nesting species were present: grey heron, cattle egret, black-crowned night heron *Nycticorax nycticorax* and little egret *Egretta garzetta* (LEKUONA, 1993).

The heronry was situated in the delta of the L'Eyre River. All the nests were located on trees: pines *Pinus pinaster*, oaks *Quercus robur*, willows *Salix atrocinerea* and on an American bush *Baccharis halimifolia* introduced in Europe. In 1992 and 1993, 330 and 320 pairs of grey heron nested in this colony respectively (LEKUONA & CAMPOS, 1995).

Sessions were carried out on two fixed days a week, from February to June 1992, and from March to June 1993. Observations were made from a blind with the aid of a 20x60 telescope. The blind was at a distance of 50 m from the colony. Nests were numbered on a photograph. Each observation session lasted a complete daylight period (from sunrise to sunset) and every 10 minutes the activity of a maximum of 15 pairs was simultaneously recorded. Time, copulatory behaviour, number of intra- and extra-pair copulation attempts, outcome (successful or not) and identity of the herons involved were recorded. Taking into account the reproductive behaviour of the grey heron (MILSTEIN et al., 1970; CRAMP & SIMMONS, 1977; VOISIN, 1991), its breeding cycle was divided in six different periods: pair formation/nest construction (two weeks), egg-laying [eight-10 days, because the eggs are generally laid at two-day intervals and clutches of four eggs are the most common, VOISIN (1991)], incubation (25-28 days), guardian period (26-31 days), post-guardian period (chicks with more than three weeks old) and fledgling period (eight weeks after hatching). The fertile period of the female herons was defined as the period from pre-laying to the

laying of the penultimate egg (BIRKHEAD & MØLLER, 1992; AGUILERA, 1994).

Since grey herons do not show any distinct sexual dimorphism (BAKER, 1982), each bird's sex from observations of intra-pair copulation was determined. That the male heron always mounted the female was assumed. Individual birds were recognized by the different colour patterns on the head and neck (VAN VESSEM & DRAULANS, 1986).

All results were compared by means of  $\chi^2$ -test of differences in frequency distribution using Yates correction, when necessary, and considered significant from the 95% level (SOKAL & ROHLF, 1979).

## Results

The copulatory behaviour of grey heron in this colony was very similar to that recorded by MILSTEIN et al. (1970). The male heron

mounts the female with open wings, female heron raises her tail, and the male rubs his cloaca on the female's while opening his bill and seizing the female's neck. All individual birds involved in extra-pair copulations were adult herons.

In 1992, 166 nests (50.3% of all nests in the colony,  $n = 330$ ) and in 1993, 163 nests (50.9% of all nests in the colony,  $n = 320$ ) were studied. During these two breeding periods which heron was the male and which was the female in 29 nests (15 in 1992 and 14 in 1993) were determined, taking into account the different colour pattern (grey feathers) in the head and neck. In 27 nests (93.1%) the heron showing this colour pattern was the female. In 1992 and 1993 most breeding pairs were formed by two adult birds ( $\geq 3$  years), 91.1% and 92.1% of all studied nests, respectively.

Figures 1 and 2 show the daily distribution of intra- and extra-pair copulation at-

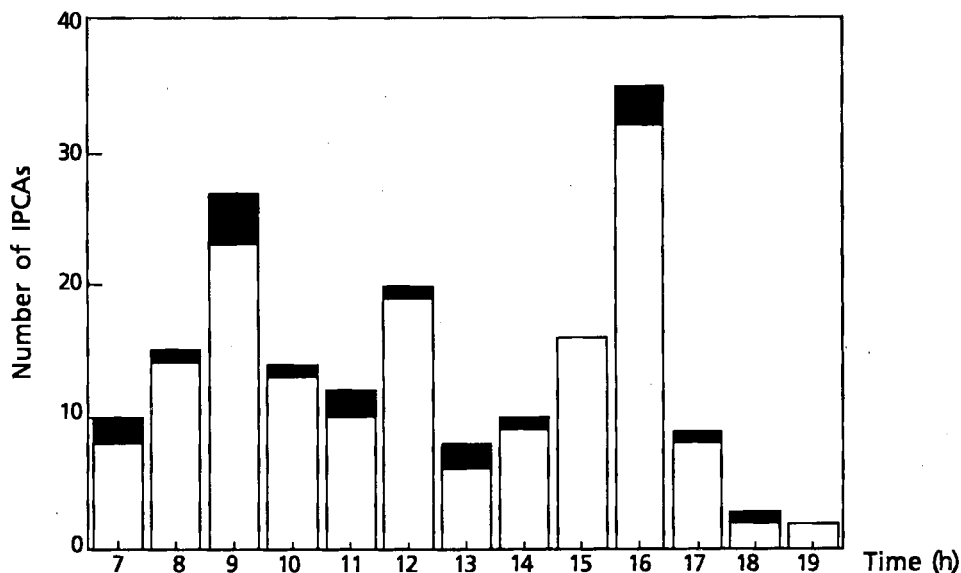


Fig. 1. Daily distribution of intra-pair copulation attempts (IPCA) in the grey heron colony in Arcachon Bay during two breeding periods (1992-1993): successful (white); unsuccessful (black).

*Distribución diaria de los intentos de cópula intrapareja (IPCA) en la colonia de garza real en la bahía de Arcachón durante dos periodos de reproducción (1992-1993): éxito (blanco); fracaso (negro).*

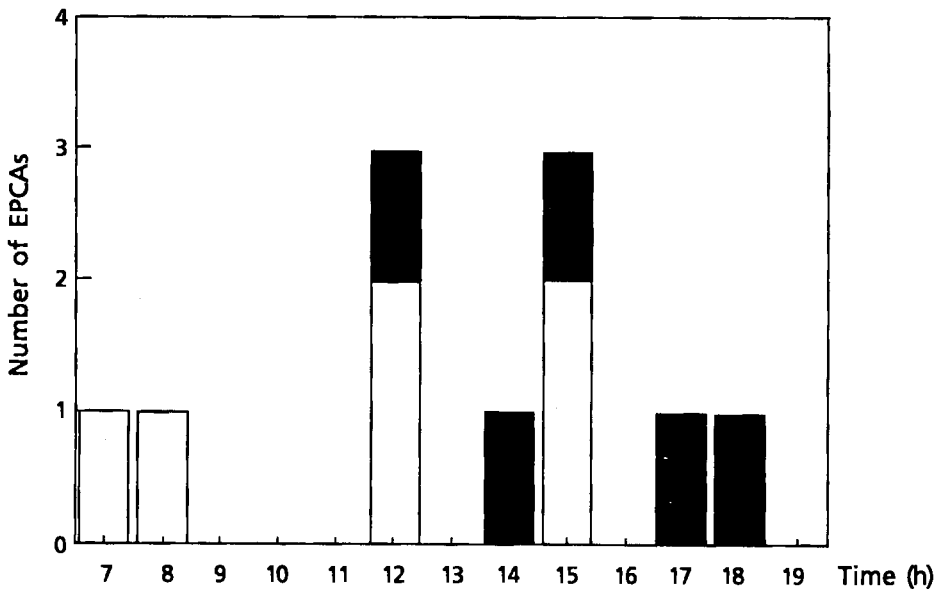


Fig. 2. Daily distribution of extra-pair copulation attempts (EPCAs) in the grey heron colony in Arcachon Bay during two breeding periods (1992-1993): successful (white); unsuccessful (black).

*Distribución diaria de los intentos de cópula extrapareja (EPCAs) en la colonia de garza real en la bahía de Arcachón durante dos periodos de reproducción (1992-1993): éxito (blanco); fracaso (negro).*

tempts. There were three intra-pair copulation attempt peaks: the first in the morning ( $n = 27$ ), the second at midday ( $n = 20$ ) and the third in the afternoon ( $n = 35$ ). Fifty-eight per cent of the unsuccessful attempts (intra- and extra-pair copulations) were made in the morning and 42% in the afternoon ( $\chi^2 = 10.1$ , 1gl,  $P < 0.001$ ).

A total of 192 copulation attempts were observed, 181 (94.3%) were intra-pair copulation attempts, and 11 (5.7%) were extra-pair copulation attempts. All extra-pair attempts were observed in 11 different controlled nests in the colony. In the morning (6.00-12.00) 103 intra and extra-pair copulation attempts were recorded (53.6%), and 89 (46.4%) in the afternoon (12.00-19.45) (without significant differences,  $\chi^2 = 0.80$ , 1gl, n.s.).

A total of 162 successful intra-pair copulations (89.5%,  $n = 181$ ) were observed and 10.5% were unsuccessful (fig. 1). During

the study period a total of six successful extra-pair copulations were recorded (54.5%,  $n = 11$ ) and 45.5% were unsuccessful. Five unsuccessful extra-pair copulations were observed and four were made in the afternoon (fig. 2). Successful extra-pair attempts were more frequently made in the afternoon. All occurred on the female heron nest. Significant differences were observed between the rate of intra- and extra-pair successful attempts ( $\chi^2 = 49.7$ , 1gl,  $P < 0.001$ ).

Ten of eleven male herons involved in extra-pair copulation attempts were paired and have their nests (most with eggs) close to their respective target female nests (< 50 m). Male grey herons left their own nests and eggs and tried to copulate with a female on a nearby nest, but the target female never cooperated. Only one male involved in EPCAs was an unmated male, showing grey feathers both on the head and

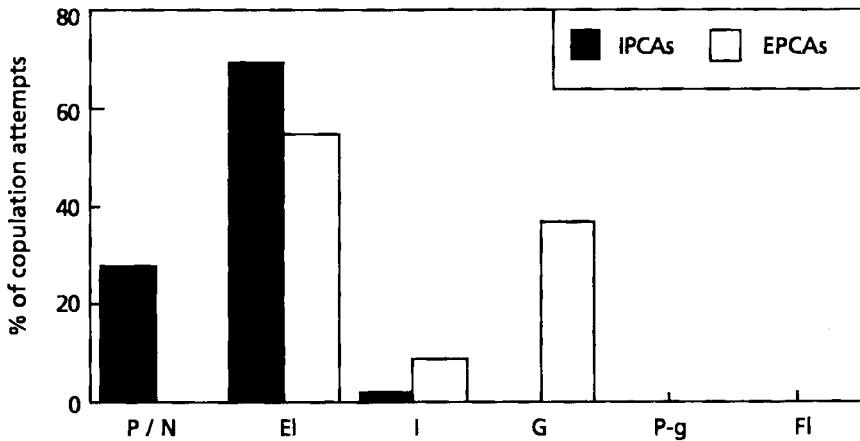


Fig. 3. Distribution of intra-pair (IPCAs) and extra-pair (EPCAs) copulations attempts during the breeding cycle of the grey heron in Arcachon Bay. Data are percentages: P/N. Pair formation/nest construction; El. Egg laying; I. Incubation; G. Guardian; P-g. Post-guardian; Fl. Fledgling.

*Distribución de los intentos de cópula intrapareja (IPCAs) y extrapareja (EPCAs) a lo largo del ciclo reproductor de la garza real en la Bahía de Arcachón. Los datos son porcentajes: P/N. Formación de pareja/construcción del nido; El. Periodo de puesta; I. Incubación; G. Periodo de guardia; P-g. Periodo de post-guardia; Fl. Volantones.*

neck. Sixty-nine per cent of intra-pair and 54.5% of extra-pair copulation attempts were made during the egg-laying period of the females. All extra-pair copulations were made during the fertile period of the target female herons and during the incubation and guardian periods of the males (fig. 3). In both study breeding periods, all attacked females had arrived at the colony later than the respective females of the male herons involved in extra-pair attempts ( $2.80 \pm 0.63$  weeks,  $n = 11$ ).

Two females (18.2% of all extra-pair copulation attempts) immediately abandoned the nests during their egg-laying period and flew away to form the colony after the extra-pair copulation attempt, and were never observed again. In all cases of extra-pair copulation attempts, females performed a behaviour including a distinctive call. In 36.4% of these cases, the male was attracted by the female calls and caused unsuccessful extra-pair copulation attempts. The male heron then made some successful copulation attempts. This dis-

tinctive call of the female herons might therefore have had a male-attracting function, when mates were near the colony, as has been recorded by FUJIOKA & YAMAGISHI (1981) and RAMO (1993). During all extra-pair copulation attempts, other adult herons located near the nest in question made antagonistic displays to the foreign male [soft calls, all plumes raised, Arch-neck Upright display and Forward-display as Threat, CRAMP & SIMMONS (1977)] defending their sites in the colony from intruders. In six cases, a furious attack on these extra-pair males by the mate of the raped female was observed.

## Discussion

The percentage of successful intra-pair copulation attempts was 89.5%, very similar to that recorded by RAMO (1993) in the heronry located in Doñana National Park (SW Spain, 84%).

Some authors (WESNEAT et al., 1990; BIRKHEAD & MØLLER, 1992; RAMO, 1993) have considered

that the nesting density and numbers of breeding pairs present in a colony are two important factors in the extra-pair copulation incidence, because there are more breeders surrounded by neighbours, but an additional increase in the breeding density does not necessarily affect the chances for this copulatory behaviour in the White Ibis (FREDERICK, 1987). RAMO (1993) (table 1) argued that in the colony of Doñana, the high nest density on trees affected the high number of extra-pair copulations. In the colony of Arcachon Bay, there was a high breeding density (330 and 330 pairs of grey herons in 1992 and 1993, respectively) but with low density of nests per tree (1.9) (LEKUONA, 1993). A lower rate of extra-pair copulation attempts than at the Doñana colony were observed. The cork oak was the tree most frequently used by grey herons for placing their nests, and its large canopy allows the settlement of a great number of nests, but at Arcachon all trees (pines, oaks, willows and bushes) have a small canopy and a heron nest was surrounded by few neighbours.

The daily distribution of intra- and extra-pair copulation attempts recorded in the colony of Arcachon Bay was not equally frequent throughout the day and could probably show different periods of female herons fertility, denominated "insemination

windows" (BIRKHEAD et al., 1987). An insemination window exists for about an hour after the egg-laying has occurred, during which time the next egg to be laid can be fertilized. In some birds, males appear to time their extra-pair copulations to coincide with these insemination windows. These authors revealed that 28 genera of birds copulated most frequently in the early morning, later in morning and in the evening. Since most bird species lay early in the morning (SKUTCH, 1952; SCHIFFERLI, 1979; TULLET, 1985), both intra- and extra-pair copulations are predicted to occur during this time of the day. BIRKHEAD et al. (1987) and AGUILERA & ÁLVAREZ (1989) suggest that if male birds are uncertain about when their partners will ovulate, it will be in their interest to copulate most frequently around dawn in order to coincide with the insemination window, when their females eventually ovulate.

Male white spoonbills attempted extra-pair copulations most frequently in the late afternoon around the egg laying time, whereas intra-pair copulations were performed throughout the day without any clear pattern (AGUILERA & ÁLVAREZ, 1989). Similar extra-pair data were found in the study colony.

In the Arcachon Bay heronry, only 5.7% of copulation attempts were made by extra-pair males. This figure is lower than that recorded by RAMO (1993) and higher than that observed by MARION (1979) (table 1). Our data agree with the mixed reproductive strategy in the grey heron (TRIVERS, 1972; BIRKHEAD & MØLLER, 1992; RAMO, 1993) since most males involved in extra-pair copulations were paired and the forced copulation occurred during the presumed fertile period of the target females, who had arrived later at the colony. In colonial bird species such as grey heron, males engage in extra-pair copulations while guarding their nest sites. These two activities are therefore not mutually exclusive in colonial birds. In our study area male herons defended their partners when they were present, but these birds engaged in extra-pair copulations when their females were absent. Our data agree with the observations on both fulmar *Fulmarus glacialis* and common guillemot *Uria aalge*'s males made by BIRKHEAD et al. (1985) and HATCH (1987).

Female grey herons involved in extra-pair copulations never cooperate. However, the

Table 1. Density of nest per tree, and number of intra- and extra-pair copulation attempts recorded at different colonies in Europe.

*Densidad de nidos por árbol y número de intentos de cópula intra- y extrapareja registrados en diferentes colonias de Europa.*

Author	Nest/tree	Intra/extra
VERWEY (1930)	2	?/10
MILDSTEIN et al. (1970)	2.1	41/0
MARION (1979)	1.1-2.39	37/1 (2.6%)
RAMO (1993)	10.3-22.5	262/39 (13.0%)
This paper	1.9	181/11 (5.7%)

resistance to extra-pair copulations may be a way that females either test the quality of males or stimulate male-male competition (COX & LeBOEUF, 1977). In other species of birds with female-accepted extra-pair copulations the dominance rank of the male is a characteristic which has sometimes been found to be important (FUJIOKA & YAMAGISHI, 1981; FREDERICK, 1987; SMITH, 1988).

In a few cases, the male herons were attracted by their female's calls and caused unsuccessful extra-pair copulation attempts. After that, the pairs made some successful copulations. These two facts can be explained taking into account the following possibilities: some grey heron males collect nest material closer to the nest during their female's fertile period as with the spoonbill (AGUILERA & ÁLVAREZ, 1989); and the sperm-devaluation hypothesis which proposes that copulations are more frequent when the risk of extra-pair copulations are high, and predicts that the sperm from frequent copulations may devalue the sperm of possible competitors (BIRKHEAD & MØLLER, 1992).

The incidence of this behaviour may also be affected by other factors: 1. Some herons involved in extra-pair copulations are likely adult males without a mate, and they use this strategy for breeding; 2. Most of these herons would be paired and would use the mixed reproductive strategy during the fertile period of female herons to increase their paternity; 3. The extra-pair copulations could play an important role in suppressing the negative impact of sterile males, as VOISIN (1976) observed in the little egret. Our data agree with the two first possibilities.

Future works about this breeding behaviour are needed, with an intense study of the activities of males in the colonies: ringing birds, DNA fingerprinting or some biomolecular techniques (BIRKHEAD & MØLLER, 1992).

## Resumen

*Cópulas extrapareja de la garza real (Ardea cinerea) en la bahía de Arcachón (SO Francia)*

En una colonia de garza real (*Ardea cinerea*), situada en la costa Atlántica francesa (bahía de Arcachon), se ha estudiado el comportamiento de cópula de las garzas durante dos

periodos de reproducción (1992-1993). Se registraron un total de 181 intentos de cópula intrapareja y 11 intentos de cópulas extrapareja (5,7% del total de intentos de cópula observados). Diez de los machos adultos involucrados en los intentos extrapareja estaban emparejados y poseían un nido en la colonia. El 89,5% de los intentos de cópula intrapareja y el 54,5% de los extrapareja tuvieron éxito. Se han observado tres picos de máxima realización de cópulas intrapareja (fig. 1) uno a la mañana, otro al mediodía y otro a la tarde. Los intentos de cópula extrapareja fueron más abundantes a la tarde (fig. 2). En dos de los casos de cópula extrapareja, las hembras abandonaron definitivamente el nido después del intento de cópula, cuando se encontraban en el periodo de puesta. Todas las cópulas extrapareja observadas se han producido durante el periodo de puesta de la hembra atacada y durante los periodos de incubación y guardia de los machos (fig. 3). En la colonia estudiada, la densidad de nidos por árbol no parece haber influido en la frecuencia de aparición del comportamiento de cópulas extrapareja (tabla 1).

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## References

- AGUILERA, E., 1994. Parental roles in the White Spoonbill (*Platalea leucorodia*): The sperm competition hypothesis. *Ardeola*, 41: 19-28.
- AGUILERA, E. & ÁLVAREZ, F., 1989. Copulations and mate guarding of the Spoonbill (*Platalea leucorodia*). *Behaviour*, 110: 1-22.
- BAKER, K., 1982. Guide to aging and sexing non-passerines; part 6: Grey Heron. *Ringers Bull.*, 6: 17.
- BIRKHEAD, T. R., ATKIN, L. & MØLLER, A. P., 1987. Copulation behaviour of birds. *Behaviour*, 101: 101-138.

- BIRKHEAD, T. R., JOHNSON, S. D. & NETTLESHIP, D. S., 1985. Extra-pair matings and mate guarding in the common murre *Uria aalge*. *Anim. Behav.*, 33: 608-619.
- BIRKHEAD, T. R. & MØLLER, A. P., 1992. *Sperm competition in birds*. Academic Press, London.
- COX, C. R. & LEBŒUF, B. J., 1977. Female incitation of male competition: a mechanism of male selection. *Am. Nat.*, 111: 317-335.
- CRAMP, S. & SIMMONS, K. E. L., 1977. *The Birds of the Western Palearctic*. Vol. 1. Oxford University Press, Oxford.
- FREDERICK, P. C., 1987. Extrapair copulations in the mating system of the White Ibis (*Eudocimus albus*). *Behaviour*, 100: 170-201.
- FUJIOKA, M. & YAMAGISHI, S., 1981. Extra-pair and pair copulations in the Cattle Egret. *Auk*, 98: 134-144.
- GLADSTONE, D. E., 1979. Promiscuity in monogamous colonial birds. *Am. Nat.*, 114: 545-557.
- HATCH, S. A., 1987. Copulation and mate guarding in the northern fulmar. *Auk*, 104: 450-461.
- LANGLEY, C. H., 1983. Biology of the Littel Bittern in the Southwestern Cape. *Ostrich*, 54: 83-94.
- LEKUONA, J. M., 1993. Uso de hábitat, alimentación y reproducción de la Garza Real *Ardea cinerea* en la Bahía de Arcachon, Francia. Tesis de licenciatura, Universidad de Navarra.
- LEKUONA, J. M. & CAMPOS, F., 1995. Le succès de reproduction de Héron cendré (*Ardea cinerea*) dans le Bassin d'Arcachon. *Alauda*, 63: 179-183.
- MARION, L., 1979. Stratégies d'utilisation du milieu des colonies de hérons cendrés *Ardea cinerea* L. en Bretagne. Ph. D. Thesis, University of Rennes.
- MCKILLIGAN, N. G., 1990. Promiscuity in the Cattle Egret (*Bubulcus ibis*). *Auk*, 107: 334-341.
- MILSTEIN, P. LE S., PRESTT, I. & BELL, A. A., 1970. The breeding cycle of the Grey Heron. *Ardea*, 58: 171-257.
- RAMO, C., 1993. Extra-pair copulations of Grey Herons nesting at high densities. *Ardea*, 81: 115-120.
- RAMO, C. & BUSTO, B., 1985. Comportamiento reproductivo del corocoro (*Eudocimus ruber*). *Mem. de la Soc. de Cien. Nat. La Salle*, 45: 77-113.
- SCHIFFERLI, L., 1979. Warum legen Singvögel (Passeres) ihre Eier am frühen Morgen? *Orn. Beob.*, 76: 33-36.
- SKUTCH, A. F., 1952. On the hour of laying and hatching of bird's eggs. *Ibis*, 94: 49-61.
- SMITH, S. M., 1988. Extra-pair copulations in black-capped chickadees: the role of the female. *Behaviour*, 107: 15-27.
- SOKAL, R. R., & ROHLF, F. J., 1979. *Biometria*. Ed. Blume, Barcelona.
- TORTOSA, F. S. & REDONDO, T., 1992. Frequent copulations despite low sperm competition in White Storks (*Ciconia ciconia*). *Behaviour*, 121: 288-315.
- TRIVERS, R. L., 1972. Parental investment and sexual selection. In: *Sexual selection and the descent of man*: 136-179 (B. Campbell, Ed.). Aldine, Chicago.
- TULLET, S. G., 1985. Laying. In: *A Dictionary of Birds*: 320-322 (B. Campbell & E. Lack, Eds.). Poyer, Calton.
- VAN VESSEM, J. & DRAULANS, D., 1986. Nest attendance by male and female Grey herons. *J. Field Ornithol.*, 57: 34-41.
- VERWEY, J., 1930. Die Paarungsbiologie des Fischreihers. *Zool. Jb. allg. Zool. Physiol.*, 48: 1-120.
- VOISIN, C., 1976. Etude du comportement de l'Aigrette garzette (*Egretta garzetta*) en période de reproduction. *L'Oiseau et R.F.O.*, 46: 387-425.
- 1991. *The Herons of Europe*. T. & A. D. Poyser, London.
- WESNEAT, D. F., SHERMAN, P. W. & MORTON, M., 1990. The ecology and evolution of extra-pair copulations. *Curr. Ornithol.*, 7: 331-369.