THE JOURNAL OF RAPTOR RESEARCH

A QUARTERLY PUBLICATION OF THE RAPTOR RESEARCH FOUNDATION, INC.

VOL. 37 MARCH 2003 NO. 1

J Raptor Res. 37(1):1–7

© 2003 The Raptor Research Foundation, Inc.

COPULATION BEHAVIOR OF A POTENTIALLY DOUBLE-BROODED BIRD OF PREY, THE BLACK-WINGED KITE (*ELANUS CAERULEUS*)

JUAN J. FERRERO,[1] JUAN M. GRANDE, AND JUAN J. NEGRO[2]

Department of Applied Biology, Estación Biológica de Doñana (CSIC), Pabellón del Perú, Avda. Mª. Luisa s/n 41013, Sevilla, Spain

ABSTRACT.—Raptors show high copulation rates when compared to other birds. This fact has been generally attributed to sperm competition. However, copulation rates in raptors tend to be seasonally bimodal, with an early peak outside the female's fertile period that cannot be explained by the sperm competition hypothesis. We studied the copulation behavior of the Black-winged Kite (*Elanus caeruleus*), that, unlike raptors previously studied, may raise two broods consecutively in the same breeding season. The first recorded copulation occurred 44 d prior to the onset of laying and the last one on d 66 after. We observed three seasonal peaks in copulation frequency. The first two peaks (40 and 10 d before egg laying, on average) correspond to the normal pattern in raptors. To explain the first peak, we propose three hypotheses: (1) pair bonding, (2) mate assessment, and (3) territorial signaling. Unfortunately, we have been unable to elaborate further predictions that would distinguish among these three hypotheses. The second peak, during the fertile period, may be attributed to sperm competition. The third peak, previously unreported in raptors, occurred 50 d after the onset of laying, the mean time lag between first and second clutches in the area. These late copulations, which were also performed by pairs that laid one clutch, may reflect the propensity of the species to lay second clutches (we recorded six replacement clutches and five second clutches out of 98 breeding attempts). This third peak of copulations may also have a fertilization function and may be related to sperm competition.

KEY WORDS: *Black-winged Kite*; Elanus caeruleus; *copulation behavior*; *sperm competition*; *territorial signaling.*

COMPORTAMIENTO COPULATORIO DE UNA RAPAZ CON DOBLE NIDADA POTENCIAL: EL ELANIO COMÚN (ELANUS CAERULEUS).

RESUMEN.—Las aves rapaces suelen presentar altas tasas copulatorias cuando se las compara con otras aves. Este hecho ha sido generalmente atribuido a la competencia espermática. Sin embargo, la tasa de cópulas en aves rapaces tiende a presentar un patrón estacional bimodal, con un primer pico antes del periodo en que la hembra es fértil, que no puede ser explicado por esta hipótesis. En este trabajo estudiamos el comportamiento copulatorio del elanio común (*Elanus caeruleus*), que a diferencia de las otras rapaces previamente estudiadas puede sacar adelante dos polladas consecutivas en la misma temporada de cría. La primera cópula se observó 44 días antes del inicio de la puesta y la última 66 días después. Observamos tres picos en la frecuencia copulatoria a lo largo de la temporada de cría. Los primeros dos (alrededor de los días 40 y 10 antes de la puesta) corresponden al patrón observado en otras rapaces. Para explicar el primer pico proponemos que se consideren tres hipótesis: (1) reforzamiento de los lazos de pareja, (2) valoración de la calidad del compañero y (3) señalización del territorio. Desafortunadamente, no hemos podido elaborar predicciones que permitan distinguir entre estas

---

[1] Present address: Tirso de Molina, 14, Mérida 06800, Badajoz, Spain.

[2] Corresponding author's e-mail address: negro@ebd.csic.es

tres hipótesis. El segundo pico, durante el periodo fértil de la hembra podría atribuirse a fenómenos de competencia espermática. El tercero, observado por primera vez en rapaces, ocurrió 50 días después del inicio de la puesta, lo que coincide con el intervalo medio entre primeras y segundas puestas en la zona de estudio. Este tercer pico, que también se detectó en aquellas parejas que solo hicieron una puesta, podría reflejar una propensión en esta especie a realizar segundas puestas (encontramos seis puestas de reemplazo y cinco segundas puestas en 98 intentos de cría). Este tercer pico de cópulas estaría probablemente relacionado con la competencia espermática.

[Traducción de los autores]

The copulation behavior of birds has been a popular research topic among behavioral ecologists in the last two decades (e.g., Birkhead et al. 1987, Birkhead and Møller 1992). This interest has been triggered by the observation of widely variable copulation rates between species (i.e., from one to several hundred copulations in a single breeding season), and the realization, through molecular paternity assessment, that extra-pair fertilizations are common in certain species (Petrie and Kempenaers 1998).

Male birds seem to have evolved two strategies to minimize the risk of paternity loss: (1) close mate guarding (Birkhead 1979) and (2) frequent within-pair copulations to dilute the sperm of possible competitors (Birkhead et al. 1987). Most raptor species probably employ the second strategy as males typically provide food to the female throughout the pre-laying period and, therefore, are precluded from guarding their mates effectively (Møller and Birkhead 1992). Raptors show high copulation rates, although the seasonal pattern of copulations in these birds is not consistent with all predictions of the sperm-competition hypothesis. Many raptors show an early peak of copulations 20–65 d before laying, before the females are fertile (Møller 1987, Negro et al. 1992, Villarroel et al. 1998, Mougeot 2000, Negro and Grande 2001), and some species copulate after clutch completion, well into the chick-rearing period (Ellis and Powers 1982, Sodhi 1991, Holthuijzen 1992). In addition, extra-pair copulations, and also extra-pair fertilizations, are infrequent in raptors, and this again calls into question the sperm-competition hypothesis (Negro et al. 1992, 1996, Villarroel et al. 1998, Negro and Grande 2001). There are at least three alternative hypotheses for high copulation rates in raptors. The pair-bonding hypothesis (Newton 1979) states that the members of the pair copulate frequently to maintain or to reinforce the pair bond. Copulations are expected to occur all through the breeding period, but are not necessarily restricted to this period if pair bonds are maintained through the year. The mate-assessment hypothesis (Tortosa and Redondo 1992, Negro et al. 1996, Villarroel et al. 1998) states that the females may acquire information on male quality through copulations. Assuming that copulations are costly, better males would be able to copulate more often. The territorial signaling hypothesis (Negro and Grande 2001) proposes that raptors signal territory ownership to conspecifics, and possibly to other avian species, by copulating frequently and conspicuously in the defended nesting area early in the breeding season.

The Black-winged Kite (*Elanus caeruleus*; also called the common Black-shouldered Kite in the Old World literature) is a small-sized (ca. 300 g) raptorial bird widely distributed in Africa (Cramp and Simmons 1980). In southern Africa, it breeds continuously, while in other areas of Africa it breeds mostly in the spring and fall (Cramp and Simmons 1980, Brown et al. 1982, Mendelsohn 1983). The species is slowly colonizing southern Europe (Ferrero 1994, Rufino 1994). In Spain, egg-laying peaks in March (Cramp and Simmons 1980, unpubl. data), but in some years some pairs may lay eggs as early as November or as late as July (Ferrero and De Lope 2001).

Our aim with this paper is to describe the copulation behavior and pattern of Black-winged Kites. Contrary to all raptorial species previously studied, the Black-winged Kite may raise two broods in a year (Mendelsohn 1983) and could have evolved a distinct seasonal pattern of copulations (i.e., some copulations are expected to occur after the first clutch).

METHODS

We studied a breeding population of Black-winged Kites in Extremadura, southwestern Spain. The main breeding habitat used by Black-winged Kites in the area consists of fragmented semi-open Mediterranean oak forests (mainly *Quercus rotundifolia*) with an understory of cereal crops (cultivated "dehesas"; Ferrero and Onrubia 1998). The stronghold for the European population (estimated at 1000 breeding pairs [Ferrero 1994]) is located

Table 1. Number of breeding pairs for which mating behavior was monitored between 1979 and 2000.

YEAR	NO. OF PAIRS	TOTAL OBSERVATIONS (hr)
1979	13	123.4
1980	12	20.7
1987	8	46.9
1988	26	53.3
1989	12	126.9
1993	2	32.7
1995	14	44.2
1996	2	8.4
1997	6	19.2
2000	3	11.5

in the dehesas of Extremadura and the neighboring Alentejo in Portugal.

We performed behavioral observations year round on a total of 98 breeding attempts in 79 different nesting territories between 1979 and 2000 (Table 1). We observed six renesting attempts after the first clutch failed to hatch (replacement clutches) and five second clutches. The observations were performed from vantage points at 200–300 m from the nests, using spotting scopes (20–60×) and binoculars (10×). Observers completed 269 observation bouts lasting 10 min to 14 hr (mean observation period: 80 min). Given that it is unlikely to observe copulations during very short observation periods, only those bouts more than 20 min long were used to calculate copulation rate and to plot the seasonal pattern of copulations. We were unable to distinguish between successful and unsuccessful copulations, and therefore we defined a copulation as occurring when a male mounted a female. Copulations as well as other distinct behaviors, including prey transfers among pair members, chasing to intruders, aerial displays, and delivery of nest material, were recorded and timed.

Black-winged Kites in this study were not individually marked. This limitation may have resulted in the detection of intruders, and thus, observation of extra-pair copulations. Nonetheless, any intrusions by conspecifics during observations would be easily detectable, as home ranges of kites are relatively small (2–4 km^2, Mendelsohn 1983, Bustamante 1993, J. Ferrero unpubl. data), tree cover in the dehesas is sparse (3–9 trees/ha), and territorial birds may be observed continuously. In addition, Black-winged Kites are strongly territorial and intruders are evicted from the nesting areas (Mendelsohn 1983, see Results). The absence of marks may also have caused pseudoreplication due to the inclusion of data from the same pairs observed for more than one year. However, given the length of the study period (21 yr), and even considering that 13 territories were monitored twice or even three times, the long time lag between two consecutive observations in the same territory (5.8 ± 4.8 yr, on average), it is unlikely these territories were occupied by the same individuals. The remaining 65 territories were sampled once. Therefore, we believe the incidence of pseudoreplication is minimal in our analysis.

We analyzed the daily variation in copulation rates during the fertile period. In previous studies on copulation behavior of raptors, the fertile period has been assumed to start around 12 d prior to laying (Bird and Buckland 1976, Negro et al. 1992, Donázar et al. 1994, Mougeot 2000). With no data available for the Black-winged Kite, we have conservatively assumed that the fertile period started 15 d before the onset of laying and ended around 10 d after when the clutch was completed (4–5 eggs layed with an interval of 2 d between consecutive eggs in the clutch [Cramp and Simmons 1980]). For analytical purposes and given that Black-winged Kites present activity peaks at dawn and dusk (Cramp and Simmons 1980), we divided daytime into three periods: (1) from sunrise to 3 hr later, (2) midday hours (of variable duration owing to photoperiodic variation throughout the copulatory period), and (3) from 3 hr before sunset to sunset. As the copulation rate within the different observation bouts followed a Poisson distribution, we fitted a Generalized Linear Model (GLM) with Poisson errors to test for differences among the three defined daily periods.

To analyze seasonal variation, days of observation were grouped into 5-d intervals relative to the estimated onset of laying (considered as day zero), and thus, independently of the period of the year in which each pair started to breed.

To calculate hatching dates the 8th primary feather of the oldest chick of three different broods, whose hatching date was precisely known, was measured twice a week through the chicks' growing period until they were about to fledge. Using these data a linear regression of the length of the 8th primary feather on age (in days) was calculated (age = 0.1837 primary + 10.277, $r^2 = 0.9852$, $P < 0.0001$). This regression line was subsequently used to estimate hatching dates for the remaining chicks in the study. Laying date was then estimated from hatching date assuming a 31 d incubation period (del Hoyo et al 1994). Data from nests that failed early, for which we did not know the laying date, were excluded from analysis Copulations during second breeding attempts, for which observations were limited, were not considered to profile the species' seasonal-copulation pattern.

RESULTS

Copulation Behavior. Each pair of Black-winged Kites usually copulated at 3–4 exposed perching sites in the nesting territory (not further than 150 m from the nest). These perching sites tended to be high and leafless branches at the top of a tree, which along with the bold coloration of the birds (white breast and belly, bluish grey upperparts)and their noisy vocalizations made copulations very conspicuous. No copulations were recorded at the nest. Copulation duration averaged 11.01 ± 0.45 sec ($\bar{x}$ ± SE, $N = 75$).

On 161 instances, we recorded the behavior of the kites immediately before copulation took place. For 55 copulations (34.2%) we did not ob-

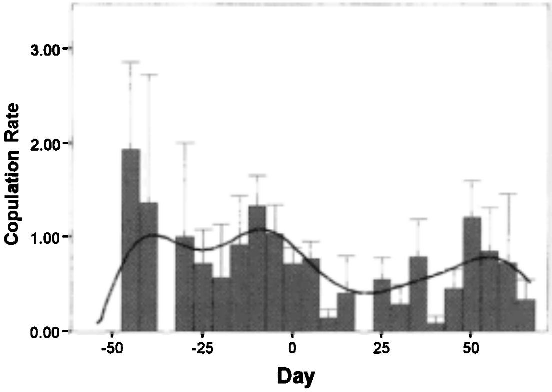

Figure 1. Mean ± SE frequency of copulation/hr of the Black-winged Kite related to the onset of laying (d 0). The line was adjusted with a normal kernel smoother.

serve any prior social behavior among mates. In some cases, two or more characteristic behaviors preceded copulation. The male transferring prey to his mate preceded 32 copulations (19.8%). On those occasions, the male waited until the female finished her meal, then flew directly onto her back and copulated. Thirty-one copulations (19.2%) were preceded by the delivery of sticks to the nest by one member of the pair. On 26 occasions (16.1%) copulations occurred shortly after aggressive encounters had taken place with intruding birds, mainly Common Buzzards (*Buteo buteo*) and Common Ravens (*Corvus corax*), which were chased away from the breeding area. Intruding Black-winged Kites were observed in 4.8% of the observation periods (13 out of 269 observation bouts). As with the other bird species, intruding kites were invariably expelled by one or both members of the pair. Only two of these intrusions by conspecifics were immediately followed by copulation of the resident pair.

Frequency and Timing of Copulations. A total of 216 copulations were observed in 487.3 hr of observation. The first recorded copulation occurred 44 d prior to the onset of laying and the last one on d 66 after the onset of laying. The maximum number of copulations seen during a single observation bout was nine in 4 hr, which occurred 12 d prior to laying a second clutch.

Using six pairs for which we have observational data on more than 10 different days, and considering daytime periods of 12 hr and a copulation period of 110 d (Fig. 1) we estimated 600.6 ± 166.2 copulations/female for the whole breeding season and 354.9 ± 98.2 for the first breeding attempt (65 d).

Combining data from the different pairs under investigation, but excluding those that laid a second clutch (see Methods), a trimodal pattern emerged in daily copulation rates through the breeding season (Fig. 1). There was a first peak around d −40 and a second peak at d −10. Kites started to copulate again around 25 d after laying, resulting in a third copulation peak around d 50, almost coinciding with the mean dates of replacement clutches (53.83 ± 4.04 d after laying date of the first clutch, $N = 6$) and close to the mean date for second breeding attempts (second laying date, 62 ± 3.76 d after laying date of the first clutch, $N = 4$). We failed to find differences in copulation rates between the three defined daily periods (i.e., 3 hr post sunrise, midday and 3 hr to sunset), as the change in deviance of the GLM was not significant ($P = 0.36$). No copulations were detected in twilight, despite the fact that the kites were observed hunting frequently at these times.

DISCUSSION

Patterns of Copulation. Copulations in the Black-winged Kite were conspicuous, and thus, easily detectable. Copulations were distributed throughout the daytime, and were not necessarily associated to other social behaviors such as mate feeding. The two peaks in copulation frequency before and during the presumed fertile period of female Black-winged Kite have previously been observed in other raptors (Møller 1987, Negro et al. 1992, Pandolfi et al. 1998, Villarroel et al. 1998, Mougeot 2000). The third peak, at day +50, is reported for the first time in raptors, although it was anticipated due to the relative frequency of second clutches among Black-winged Kites. Considering only the copulations performed during a single breeding attempt (presumably the first one in the majority of pairs that we studied), copulation rates were high and in the range found in other diurnal raptors (see references above, also Balgooyen 1976, Rosenfield et al. 1991, Korpimäki et al. 1996). Our estimate for the Black-winged Kite (around 5.5 copulations/d) is similar to that reported by Van Der Merwe (1980) for a pair in South Africa (7 copulations/d in a 15-d period during nest building).

As we already discussed (see Introduction), the first peak in copulation frequency around 40 d prior to laying is unlikely related to fertilization, as it probably occurs well before the female's fertile period. Alternative hypotheses, such as mate-assessment or strength of the pair bond hypotheses predict higher copulation rates at the time of pair formation or pair reunion, but are difficult to test. The territory-signaling hypothesis predicts frequent and conspicuous copulations when a pair establishes a breeding territory (Negro and Grande 2001). In the Black-winged Kite, copulations are indeed very frequent and almost always occur on conspicuous perches. The frequency of copulations immediately preceded by agonistic encounters with other bird species or conspecifics is not negligible (16%). Our data seem to support the territory-signaling hypothesis as a possible explanation for the early peak in copulations as suggested for most diurnal raptors (Negro and Grande 2001), but we cannot discard either the pair-bond or the mate-assessment hypotheses.

The second peak in copulation frequency, at the beginning of the female's fertile period, may be related to sperm competition pressures. However, some aspects of the kite's behavior seem to indicate low levels of sperm competition during this second peak. First, as in other frequently-copulating birds (Tortosa and Redondo 1992, Birkhead and Møller 1993, Bertran and Margalida 1999), the copulation rate decreased from beginning to end of the fertile period. In the context of sperm competition, copulation rates should be highest at the onset of laying (Birkhead 1988, Birkhead and Møller 1992, but see Birkhead and Møller 1993). Two intrusions of Black-winged Kites followed by copulation of the resident pair occurred during the fertile period. However, intrusions by conspecifics do not seem to be frequent, at least in our study area. Bustamante (1993) found only six intrusions in 146 hr of observation (0.04 intrusions/hr), and we found just 13 in 487 hr (0.03 intrusions/hr), which is similar to that found in the Merlin (*Falco columbarius,* 0.02–0.05 intrusions/hr, Sodhi 1991). Mougeot (2000) reported higher frequencies of intrusions for the Red Kite (*Milvus milvus,* 0.7–4 intrusions/hr).

Copulations After the First Nesting Attempt: Renesting, Second Clutches or Sequential Polyandry? The most remarkable finding of our study is the existence of a third peak in copulation frequency later in the breeding season, close to the fledging time of the young produced in the first breeding attempt. In some raptors, copulations cease at the end of laying or close to it (Newton 1986, Birkhead and Lessells 1988, Negro et al. 1992, Mougeot 2000). In other species the occurrence of copulations during incubation or even during the nestling period are not uncommon (Ellis and Powers 1982, Holthuijzen 1992, Donázar et al. 1994, Pandolfi et al. 1998). Nonetheless, we know of no other raptor species in which late copulations reached similar rates to those of the pre-laying period, as we found in this study. Copulations after clutch completion are suggested to be a preventive behavior to speed up a replacement clutch if the first one is lost (Birkhead et al. 1987). But renesting attempts are scarce among raptors, especially in larger ones (Newton 1979, Mundy et al. 1992, Martínez et al. 1998). Second breeding attempts are even rarer, but do occur in some species (Newton 1979, Toland 1985). In the Iberian Peninsula only the Eurasian Kestrel (*Falco tinnunculus*) has been observed raising a second brood in the same year (Sánchez 1990, Fargallo et al. 1996). When conditions permit, the Black-winged Kite may breed two or more times in a year (Mendelsohn 1983). Appropriate conditions do not seem to be common in Spain but they do occur, as we observed five second-breeding attempts. In small birds, such as passerines, both replacement clutches and multiple breeding attemps are common (e.g., Møller 1985), and therefore, copulations are expected in these species after the first breeding attempt. However, we have found no analysis on the seasonal pattern of copulations in multiple-brooded species.

The coincidence of the third peak in copulation rates with the dates of replacement or double clutches may be an adaptation related to the tendency of the Black-winged Kite to initiate a second breeding attempt, which they may abort just before laying if food conditions are not adequate. Although data on female's fertility in this period are lacking, it may be argued that these copulations occur in a fertilization context and sperm competition might play a role.

The unusual early laying dates that we recorded in some years (i.e., November or December, Ferrero and De Lope 2001) seem to indicate that independently of seasonal photoperiodic and climatic variation of the temperate zones, Black-winged Kites may try to breed if other factors (most probably food abundance) are favorable.

Bustamante (1993), in a study carried out in the same area, found that two radiotagged adult females had left the nest well before the nestlings became independant, whereas the male fed the young until they dispersed from the territory. In three other pairs (with unmarked birds) this author was unable to conclude if both adult birds remained in the territory or not. We have also found some evidence of only one adult remaining until the young fledge, but this does not exclude the possibility that other pairs remain together and initiate a second breeding attempt. In fact, we did not find any evidence of mate switching (temporal disappearance of one of the pair members) in the six renesting attempts, and at least in one of the second breeding attempts both members of the pair fed the young of the first brood while copulating and constructing the second nest in a neighboring tree. Unfortunately, as our birds were not marked, we cannot conclude if renesting or second breeding attempts (and therefore the third copulation peak) are performed by the same mates, or as occurs in South Africa (and in Australia by the Letter-winged Kite, *Elanus scriptus*), the female involved in the male's second attempt is a different individual (Mendelsohn 1983, Marchant and Higgins 1993).

ACKNOWLEDGMENTS

The late F. Carbajo initiated this study and participated in early observations. We are indebted to P. Gómez, M. Cortés, M. Cabrero and J.A. Román for their assistance in different periods of fieldwork. V. Pizarro, L. Lozano, and M.G. Calzado shared with us their wide knowledge on kites' behavior. We thank J. Seoane for the amount of precious time he wasted with us during data analysis. F. de Lope, J. Avilés, B. Arroyo, D. Parejo, T. Birkhead, and an anonymous reviewer improved an early version of the manuscript with their comments. Fieldwork was carried out with no institutional financial support.

LITERATURE CITED

BALGOOYEN, T.G. 1976. Behavior and ecology of the American Kestrel (*Falco sparverius* L.) in the Sierra Nevada of California. Univ. Calif. Publ. Zool. 103:1–83. Berkeley, CA U.S.A.

BERTRAN, J. AND A. MARGALIDA. 1999. Copulatory behavior of the Bearded Vulture. *Condor* 101:164–168.

BIRD, D.M. AND R.B. BUCKLAND. 1976. The onset and duration of fertility in the American Kestrel. *Can. J. Zool.* 54:1595–1597.

BIRKHEAD, T.R. 1979. Mate guarding in the Magpie *Pica pica*. *Anim. Behav.* 27:866–874.

———. 1988. Behavioral aspects of sperm competition in birds. *Adv. Stud. Behav.* 18:35–72.

——— AND C.M. LESSELLS. 1988. Copulation behavior of the Osprey *Pandion haliaetus*. *Anim. Behav.* 36:1672–1682.

——— AND A.P. MØLLER. 1992. Sperm competition in birds. Academic Press, London, U.K.

——— AND ———. 1993. Why do male birds stop copulating while their partners are still fertile? *Anim. Behav.* 45:105–118.

———, L. ATKIN, AND A.P. MØLLER. 1987. Copulation behavior of birds. *Behavior* 101:101–138.

BROWN, L.H., E.K. URBAN, AND K. NEWTON. 1982. The birds of Africa. Vol. 1. Academic Press, London, U.K.

BUSTAMANTE, J. 1993. The post-fledging dependence period of the Black-shouldered Kite (*Elanus caeruleus*). *J. Raptor Res.* 24:185–190.

CRAMP, S. AND K.E.L. SIMMONS. 1980. Handbook of the birds of Europe, the Middle East and North Africa. Vol. 2. Oxford Univ. Press, Oxford, U.K.

DEL HOYO, J., A. ELLIOTT, AND J. SARGATAL. 1994. Handbook of the birds of the world. Vol. II. Lynx Edicions, Barcelona, Spain.

DONÁZAR, J.A., O. CEBALLOS, AND J.L. TELLA. 1994. Copulation behavior in the Egyptian Vulture. *Bird Study* 41:37–41.

ELLIS, D.H. AND L. POWERS. 1982. Mating behavior in the Golden Eagle in non-fertilization contexts. *Raptor Res.* 16:134–136.

FARGALLO, J.A., G. BLANCO, AND E. SOTO-LARGO. 1996. Possible second clutches in a Mediterranean montane population of the Eurasian Kestrel (*Falco tinnunculus*). *J. Raptor Res.* 30:70–73.

FERRERO, J.J. 1994. Situación del Elanio Azul *Elanus caeruleus* en el Mediterráneo. Pages 101–115 *in* J. Muntaner and J. Mayol (EDS.), Biología y Conservación de las rapaces mediterráneas. SEO/BirdLife Monografías No. 4. Pozuelo de Alarcón, Madrid, Spain.

——— AND F. DE LOPE. 2001. Breeding phenology of Black-shouldered Kites (*Elanys caeruleus*) in Extremadura (SW Spain). Page 65 *in* M. Ferrer, J.J. Negro, and J. Bustamante (Eds.). 4th Eurasian Congress on Raptors. Book of Abstracts. Sevilla, Spain.

——— AND A. ONRUBIA. 1998. Expansión del área de cría y distribución actual del Elanio Azul *Elanus caeruleus* en España. Pages 159–171 *in* B.-U. Meyburg, R.D. Chancellor, and J.J. Ferrero [EDS.], Holarctic birds of prey. WWGBP & ADENEX, Mérida, Spain.

HOLTHUIJZEN, A.M.A. 1992. Frequency and timing of copulations in the Prairie Falcon. *Wilson Bull.* 104:333–338.

KORPIMÄKI, E., K. LAHTI, C.A. MAY, D.T. PARKIN, G.B. POWELL, P. TOLONEN, AND J.H. WETTON. 1996. Copulatory behavior and paternity determined by DNA fingerprinting in kestrels: effects of cyclic food abundance. *Anim. Behav.* 51:945–955.

MARCHANT, S. AND P.J. HIGGINS. 1993. Handbook of Australian, New Zealand, and Antarctic birds. Vol. 2. Oxford Univ. Press. Melbourne, Australia.

MARTÍNEZ, F., G. BLANCO, AND R. RODRÍGUEZ. 1998. Rate, timing, and success of clutch replacement by colonial Griffon Vultures (*Gyps fulvus*). *Ornis Fenn.* 75:145–148.

MENDELSOHN, J.M. 1983. Social behavior and dispersion of the Black-shouldered Kite. *Ostrich* 54:1–18.

MØLLER, A.P. 1985. Mixed reproductive strategy and mate guarding in a semi-colonial passerine, the swallow *Hirundo rustica. Behav. Ecol. Sociobiol.* 17:401–408.

———. 1987. Copulation behavior in the Goshawk, *Accipiter gentilis. Anim. Behav.* 35:755–763.

——— AND T.R. BIRKHEAD. 1992. A pairwise comparative method as illustrated by copulation frequency in birds. *Am. Nat.* 139:644–656.

MOUGEOT, F. 2000. Territorial intrusions and copulation patterns in Red Kites, *Milvus milvus,* in relation to breeding density. *Anim. Behav.* 59:633–642.

MUNDY, P., D. BUTCHART, J. LEDGER, AND S. PIPER. 1992. The vultures of Africa. Acorn & Russel Friedman Books. Johannesburg, South Africa.

NEGRO, J.J. AND J.M. GRANDE. 2001. Territorial signaling: a new hypothesis to explain frequent copulation in raptorial birds. *Anim. Behav.* 62:803–809.

———, J.A. DONÁZAR, AND F. HIRALDO. 1992. Copulatory behavior in a colony of Lesser Kestrels: sperm competition and mixed reproductive strategies. *Anim. Behav.* 43:921–930.

———, M.R. VILLARROEL, J.L. TELLA, U. KUHNLEIN, J.A. DONÁZAR, AND D.M. BIRD. 1996. DNA fingerprinting reveals a low incidence of extra-pair fertilizations and intraspecific brood parasitism in the Lesser Kestrel. *Anim. Behav.* 51:935–943.

NEWTON, I. 1979. Population ecology of raptors. Buteo Books, Vermillion, SD U.S.A.

———. 1986. The Sparrowhawk. T. & A.D. Poyser, Calton, UK.

PANDOLFI, M., R. PAGLIARANI, AND G. OLIVETTI. 1998. Intra- and extra-pair copulations and female refusal of mating in Montagu's Harriers. *J. Raptor Res.* 32:269–277.

PETRIE, M. AND B. KEMPENAERS. 1998. Extra-pair paternity in birds: explaining variation between species and populations. *Trends Ecol. Evol.* 13:52–58.

ROSENFIELD, R.N., J. BIELEFELDT, AND J. CARY. 1991. Copulatory and other pre-incubation behaviors of Cooper's Hawks. *Wilson Bull.* 103:656–660.

RUFINO, R. 1994. Black-shouldered Kite *Elanus caeruleus* Pages 146–147 *in* G.M. Tucker and M.F. Heath [EDS.], Birds in Europe, their conservation status. BirdLife International, Cambridge, U.K.

SÁNCHEZ, A. 1990. Noticiario ornitológico. *Ardeola* 37:335.

SODHI, N.S. 1991. Pair copulations, extra-pair copulations, and intraspecific nest intrusions in Merlin. *Condor* 93:433–437.

TOLAND, B.R. 1985. Double brooding by American Kestrel in central Missouri. *Condor* 87:434–436.

TORTOSA, F.S. AND D.T. REDONDO. 1992. Frequent copulations despite low sperm competition in White Storks (*Ciconia ciconia*). *Behavior* 121:287–315.

VAN DER MERWE, F. 1980. Nest building in the Black-shouldered Kite. *Ostrich* 51:113–114.

VILLARROEL, M., D.M. BIRD, AND U. KUHNLEIN. 1998. Copulatory behavior and paternity in the American Kestrel: the adaptive significance of frequent copulations. *Anim. Behav.* 56:289–299.

Receivd 25 March 2002; accepted 5 December 2002.