PARENTAL CARE AND BEHAVIOR OF BREEDING AMERICAN KESTRELS (FALCO SPARVERIUS) IN CENTRAL ARGENTINA

MARÍA SOLEDAD LIÉBANA¹

Laboratorio de Vertebrados, Departamento de Biología, Facultad de Ciencias Exactas y Naturales, Universidad Nacional de Mar del Plata, Funes 3350, (7600) Mar del Plata, Argentina

JOSÉ HERNÁN SARASOLA

Centro para el Estudio y Conservación de Aves Rapaces en la Argentina (CECARA), Departamento de Recursos Naturales, Facultad de Ciencias Exactas y Naturales, Universidad Nacional de La Pampa. Avenida Uruguay 151, (6300) Santa Rosa, Argentina and Consejo Nacional de Investigaciones Científicas y Técnicas de Argentina (CONICET)

María Susana Bó

Laboratorio de Vertebrados, Departamento de Biología, Facultad de Ciencias Exactas y Naturales, Universidad Nacional de Mar del Plata, Funes 3350, (7600) Mar del Plata, Argentina

ABSTRACT.—We studied reproductive parameters, agonistic interactions, foraging behavior, prey deliveries, and diet of American Kestrels (*Falco sparverius*) using nest boxes in semiarid forests in central Argentina. The breeding season (from egg-laying to fledging) began in late October and ended in late December. Average clutch size was 4.3 ± 0.3 (SE) eggs (N = 6 nests), hatching success was 73%, and nest success was 66%. Incubation was primarily by females, whereas males mostly hunted and defended the nest area. During early and late nestling stages, both sexes showed aggressive behavior against intruders. The primary hunting method we observed kestrels using near the nest box was perch-hunting (99%), with a peak in hunting activity during midday for females and during morning for males. Both sexes visited the nest most frequently during the late nestling stage (males: 1.04 ± 0.47 prey/hr; females: 1.22 ± 0.35 prey/hr), likely because of high energy demands of the nestlings for growth during that time. The majority of the nestling diet was arthropods (71.4% of diet as determined by observations; 71% by pellets; 89% by prey remains). Reproductive characteristics of this species in the semiarid forest of central Argentina, including reproductive rate, role partitioning between sexes, foraging behavior, and diet, are similar to those previously recorded for some populations in North America.

KEY WORDS: American Kestrel; Falco sparverius; Argentina; breeding behavior; diet; parental care; semiarid forest.

CUIDADO PARENTAL Y COMPORTAMIENTO DE *FALCO SPARVERIUS* EN ÁREAS DE CRÍA DEL CENTRO DE ARGENTINA

RESUMEN.—Estudiamos los parámetros reproductivos, las interacciones agresivas, el comportamiento de forrajeo, el aporte de presas por parte de los adultos y la dieta de los pichones de individuos de la especie *Falco sparverius* que se encontraban utilizando cajas de anidación ubicadas en bosques semiáridos del centro de Argentina. El período reproductivo (desde la puesta de huevos hasta el abandono de los nidos por parte de los pichones) se extendió desde finales de octubre hasta finales de diciembre. El tamaño de puesta promedio (\pm EE) fue de 4.3 \pm 0.3 huevos (N = 6 nidos), el éxito de eclosión fue del 73% y el éxito de cría fue del 66%. La incubación fue realizada en su mayor parte por las hembras, mientras que los machos principalmente cazaron y defendieron el nido. Durante las fases tempranas y tardías del período de cría, ambos sexos demostraron un comportamiento agresivo ante intrusos. La estrategia de captura más utilizada fue desde perchas (99%), con una actividad de captura (intentos y capturas exitosas) mayor durante el mediodía en las hembras y durante la mañana en los machos. Ambos sexos visitaron el nido más frecuentemente durante la fase tardía de la cría de pichones (machos: 1.04 ± 0.47 presas/h; hembras: 1.22 ± 0.35 presas/h), probablemente debido a la alta demanda energética por parte de los juveniles para su creci-

¹ Email address: soleliebana@hotmail.com

miento durante esa etapa. La mayoría de la dieta de los pichones consistió de artrópodos (egagrópilas: 71%, restos de presas: 89% y observaciones 71.4%). La estrategia reproductiva registrada para esta especie en el bosque semiárido del centro de Argentina es similar a la previamente documentada para algunas poblaciones de Norteamérica en cuanto a su tasa reproductiva, la división de roles entre sexos, el comportamiento de forrajeo y la dieta.

[Traducción del equipo editorial]

The amount of time spent by parents incubating eggs and brooding young, food provisioning rates, and defensive behaviors are variables sometimes used to assess quality of parental care in birds (Gaibani and Csermely 2007). Parents are expected to balance the costs and benefits of reproduction so that fitness is maximized (Williams 1966). In many species, the nestling period is a critical time for behavioral decisions by parents regarding the amount of effort to be invested in the current reproduction (Martins and Wright 1993).

American Kestrels (Falco sparverius) are socially monogamous birds with sex-role partitioning throughout the breeding season (Balgooyen 1976). The kestrel's breeding biology and behavior have been widely studied in North America, but only one review of its natural history in South America has been published (Venezuela; Balgooyen 1989). Although this raptor is abundant in the southernmost part of its range, its behavior and breeding biology there have received little scientific attention; most information is anecdotal (De Lucca 1992, De Lucca and Saggese 1993). The kestrel's foraging ecology and diet have been studied in Chile, Argentina, and Brazil (Yañez et al. 1980, Figueroa and Corales 2002, Sarasola et al. 2003, Figueroa and Corales 2004, Castro Cabral et al. 2006, Zilio 2006).

Our objective was to study the breeding biology of American Kestrels in Argentina and to compare this information with that for kestrels in North America. We describe parental care and foraging behavior and quantify the division of labor between sexes of American Kestrels breeding in nest boxes in the semiarid forest of central Argentina.

STUDY AREA AND METHODS

Our study was conducted in the Parque Luro Reserve $(36^{\circ}55'S, 64^{\circ}16'W)$, central Argentina. The reserve (7604 ha) is located in La Pampa province and consists mainly of xerophytic open forest of caldén (*Prosopsis caldenia*), which represents the characteristic landscape of the Espinal biome in the semiarid pampas of Argentina (Sarasola et al. 2005). These semiarid forests have hot summers and cold winters with low humidity and low annual rainfall, which falls primarily in spring and summer (Cabrera 1994).

During August 2006, we installed twelve nest boxes in available trees and on electric poles in the reserve. Nest boxes were built following the design of Bortolotti (1994) and mounted ca. 1 km apart (mean = $1.07 \text{ km} \pm 0.1$ [SE]) and >3 m aboveground. Nest boxes were monitored from October to December of 2006 (late spring to early austral summer). After we determined which nest boxes were active (defined as those where at least one egg was laid), we attempted to capture both adults associated with each box. Kestrels were captured using bal-chatri traps (Berger and Muller 1959), or by hand in the boxes while they were incubating eggs. To allow field identification of birds during observations, we marked each individual with a patagial tag displaying an alphabetic code (Varland et al. 2007).

To establish the breeding chronology of kestrels in our study area, we visited nest boxes periodically (once every 10 d) after they were considered occupied by a pair of kestrels. During nest visitation, we recorded clutch size, the number of young hatched, and the number of young fledged. Time of hatching was determined either visually during these inspections or by aging nestlings using a photographic aging key (Griggs and Steenhof 1993). Fledging success was calculated as the proportion of total active nests that fledged at least one young.

The behavior of adult kestrels was recorded during three stages of the reproductive cycle: incubation, early nestling stage (first week after hatching) and late nestling stage (the remaining 3 wk after hatching), about the time when diurnal brooding terminates (Bird and Palmer 1988, Gaibani et al. 2005). We conducted focal observations using 10×50 binoculars and a $15/45 \times 50$ spotting scope at a distance of about 100 m from the nest boxes to record foraging and breeding behavior of American Kestrels. To ensure a balanced distribution of field observations between pairs and for different times of the day, we established four time blocks: morning (08:00–11:00 H), midday (11:00–

14:00 H), afternoon (14:00–17:00 H) and evening (17:00-20:00 H; Altmann 1974). Focal observations (Altmann 1974) of adult kestrels at each nest were conducted during each time block, and the nest to be observed was randomly selected from those occupied by a kestrel pair. During observations we recorded the percentage of time incubating by each sex, the number of prey capture attempts made by adult kestrels and the results (successful or not) of those attempts. Additionally, we recorded the type of prey captured (differentiating only between vertebrate and arthropod prey), the hunting method employed (aerial or from a perch), the final recipient of the prey (consumed by the hunter or delivered to the mate or to the young at the nest), and the number of agonistic interactions with conspecifics and other avian species (Gaibani and Csermely 2007). Parental care by male and female kestrels was evaluated by recording hunting and feeding behavior as (1) the percent of all prey delivered to the nest by each parent, and (2) the number of prey items delivered per hour by each parent. In addition, we collected regurgitated pellets and prey remains found at the nest boxes, to determine the diet of nestlings and compare this information with field observations of prey delivered to nests by the adults.

RESULTS AND DISCUSSION

Nest-box Occupancy. Six of the twelve nest boxes were occupied by kestrels in 2006. Of these pairs, five females and one of the males were captured and marked. During the breeding season, two nests were predated, one at the beginning of incubation, when the female was killed as well, and the other during the early nestling stage.

Breeding Chronology and Reproductive Parameters. The breeding season of American Kestrels in our study area began in late October (24–28 Oct) and ended in late December (20-26 Dec), which was similar to the breeding chronology of American Kestrels in Argentine Patagonia (De Lucca and Saggese 1993). Average clutch size was 4.3 ± 0.3 SE eggs (N = 6 nests). Seven of 26 eggs (27%) did not hatch (three were predated and four failed to hatch) and 19 eggs hatched successfully (73%). Two nestlings were predated, another died, and a total of 16 nestlings (61%) fledged from four nests, with a sex ratio biased to females (3:1, N = 16). Nest success was 66.7% (four successful nests). These reproductive parameters were similar to those recorded for populations of American Kestrels in North

and Central America (Heintzelman and Nagy 1968, Bloom and Hawks 1983, Wilmers 1983, Toland and Elder 1987, Wheeler 1992, Varland and Loughlin 1993, Jacobs 1995).

Role of the Sexes During Incubation. We conducted 135 hr of focal observations at five nest boxes. Early in the breeding season, females devoted most of their time to incubation and brooding the young, presumably until the young were able to thermoregulate (Dunn 1979).

Males were not recorded incubating at three nests. At the two remaining nests, females accounted for 91.4% of the observations of incubation. Males mainly contributed to defense against intruders, or hunted. Male kestrels may participate in incubation for several short periods daily (Balgooyen 1976) but, as with many species, individual pairs vary in their incubation routine (Newton 1979). Our finding that female kestrels accounted for most of the incubation was similar to incubation patterns reported for kestrels in North America (Porter and Wiemeyer 1972, Bird and Palmer 1988, Kellner and Ritchison 1988, Bortolotti and Wiebe 1993).

Agonistic Behavior. During the breeding season, both members of kestrel pairs aggressively defended their nesting territories from intra- and interspecific intruders. During incubation, males accounted for all the defense activity observed (0.25 ± 0.06 interactions per hr, N = 5 pairs), but during early and late nestling stages, both sexes showed aggressive behavior against intruders (early nestling stage, males 0.37 ± 0.1 and females 0.13 ± 0.05 interactions per hr [±SE], N = 5 pairs; late nestling stage, males 0.15 ± 0.08 and females 0.17 ± 0.05 interactions per hr [±SE], N = 4 pairs).

We registered 48 interspecific and 11 intraspecific agonistic interactions. Aggressive behavior of American Kestrels was observed most often against Southern Caracaras (*Caracara plancus*; 52.1%), followed by Chimango Caracara (*Milvago chimango*; 18.8%) and other species (including Swainson's Hawk [*Buteo swainsoni*], Black Vulture [*Coragyps atratus*], and passerines; 29.1%). In all cases, the aggressor was the American Kestrel, while the other species, perhaps perceived as threats to the nestlings, remained mostly passive or flew away. The large population of Southern Caracaras, which are known nest predators at the reserve, likely explains the high percentage of interactions with this species.

Foraging Behavior and Hunting Activity. American Kestrels employ two distinct hunting methods: perch-hunting and hovering (Jaksic and Carothers

	Males (N = 5)	Females $(N = 5)$		
Time-block	CAPTURE ATTEMPTS PER HOUR	CAPTURE SUCCESS PER HOUR	CAPTURE ATTEMPTS PER HOUR	CAPTURE SUCCESS PER HOUR	
Morning (08:00–11:00 H)	2.53 ± 0.55	1.76 ± 0.48	2.53 ± 0.97	1.72 ± 0.7	
Midday (11:00–14:00 H) Afternoon (14:00–17:00 H)	1.36 ± 0.39 0.53 ± 0.16	1.15 ± 0.29 0.49 ± 0.13	3.46 ± 0.25 4.08 ± 0.36	2.66 ± 0.3 2.39 ± 0.18	
Evening (17:00–20:00 H)	0	0	1.43 ± 0.88	1.02 ± 0.73	

Table 1. Hunting activity (mean \pm SE) of male and female American Kestrels throughout the day in the semiarid forest in Parque Luro Reserve, central Argentina.

1985, Bildstein and Collopy 1987). The primary hunting method we observed kestrels using near the nest box was perch-hunting (99.3% of hunting observations, N = 5 pairs). We recorded only incidental occurrences of hovering flights (0.7% of hunting observations); these percentages were similar to those reported by Bildstein and Collopy (1987). The percentages of each hunting mode were similar for male and female kestrels in our study area (N = 5 pairs). Given that our observations were limited to the nest area, the high proportion of perch-hunting probably reflects the high availability of suitable perches there.

We recorded 327 foraging attempts by breeding kestrels in their nest areas, with a mean rate of 2.4 attempts/hr (males and females combined). Just over 72% of all recorded attempts were made by females (1.75 attempts/hr) and 27.5% were made by males (0.67 attempts/hr). This apparent female bias in foraging attempts near the nest differed from the foraging equity by male and female kestrels reported by Smallwood (1987) and the male-biased hunting activity reported by Balgooyen (1989) and Gard and Bird (1990). Our results may have underestimated hunting activity by males, because our observations of foraging attempts were restricted to the nest area.

Hunting activity as measured by the rate of capture attempts and the rate of successful captures differed among times of day for males and females. Females (N = 5) hunted more during the midday and afternoon time periods, which was expected because orthopterans, the principal prey of kestrels, increase their rate of movement as ambient temperature increases (Balgooyen 1976). Male kestrels (N = 5) were more active during the morning time period, perhaps because they hunt more vertebrate prey. Hunting activity was low for both sexes in the evening (Table 1). During incubation, 60% of the total prey captures observed (N = 25) were by male kestrels; 53% of these prey items were transferred to the female. Hunting activity was highest during the late nestling stage (Fig. 1).

Sixty-three percent of all capture attempts were successful (mean capture rate of 1.5 prey/hr), and capture success rates were similar for males and females (58.9% and 64.6%, respectively). Similar success rates have been reported for kestrel populations in California and Venezuela (Balgooyen 1976, Collopy and Koplin 1983, Balgooyen 1989).

Of 315 prey items we observed being carried to the observation area, arthropods made up 77.5% and vertebrate prey totaled about 15.5%; the remainder were unidentified. Females brought 200 prey items (87.5% arthropods and 8.5% vertebrates); 45% were consumed by the female and the remainder were delivered to nestlings. Males



Figure 1. Overall rates of capture attempts/hr and successful captures/hr (mean \pm SE) for male and female American Kestrels during all stages of the nesting cycle in semiarid forest in Parque Luro Reserve, central Argentina.

STAGE AND PREY TYPE	ME	MEAN PREY DELIVERY RATES (PREY/1	/hr)
	MALES	FEMALES	TOTAL
Early nestling stage			
Vertebrate	0.19 ± 0.05	0.13 ± 0.08	
Arthropod	0.07 ± 0.07	0.12 ± 0.03	
Total	0.34 ± 0.08	0.32 ± 0.11	0.70 ± 0.16
Late nestling stage			
Vertebrate	0.15 ± 0.06	0.08 ± 0.05	
Arthropod	0.75 ± 0.42	1.09 ± 0.34	
Total	1.04 ± 0.47	1.22 ± 0.35	2.26 ± 0.61

Table 2. Prey type and mean prey delivery rates (prey/hr \pm SE) for male and female American Kestrels in semiarid forest in Parque Luro Reserve, central Argentina during the early nestling stage (N = 5 pairs) and the late nestling stage (N = 4 pairs).

brought 115 prey items (60% arthropods and 28% vertebrates), of which they consumed 34.8% and delivered 65.2% to the female and nestlings.

Prey Deliveries. During the overall nestling period, we recorded a total of 175 food deliveries to the nestlings by male and female kestrels (N = 5 pairs; 17.7% vertebrates, 71.4% arthropods and 10.8% unidentified prey). Females contributed an average of 62.8% of these food deliveries (81.8% arthropods, 11.8% vertebrates and 6.4% unidentified), whereas the males contributed 37% (53.8% arthropods, 27.7% vertebrates and 18% unidentified). In California and Arizona, female kestrels made 71.1% and 54.0% of food deliveries, respectively (Balgooyen 1976, Coonan 1986). In our study, the mean prey delivery rate for females was 1.65 prey/hr. Males and females exhibited different rates of prey deliveries throughout the day. Maximum rates of prey delivery by males occurred during morning (1.25 \pm 0.32 prey/hr) and by females during midday $(2.63 \pm 0.61 \text{ prey/hr})$. Smith et al. (1972) reported peaks in prey delivery rates by kestrels in Utah between 09:00-12:00 H and between 16:00-17:00 H. Parrish (2007) reported a similar bimodal feeding pattern for southeastern American Kestrels in Georgia.

Prey delivery rates differed between early and late nestling stages. More frequent visits to the nest during the late nestling stage (1.13 prey/hr vs. 0.33 prey/hr during the early nestling stage) were likely due to higher energy demands of the nestlings during their late growth stage, as is the case for other avian species (Ricklefs 1968, Newton 1979, Holthuijzen 1990). Delivery rates of vertebrate prey by males were higher than those of females during both early and late nestling stages (Table 2). Of 49 vertebrate prey captured, the male was responsible for 65%.

Diet. Analysis of 26 pellets and 840 prey remains collected from nest boxes indicated that 71% of prey items in the pellets were arthropods and 29% were vertebrates (N = 117 items), whereas for the prey remains, 89% were arthropods and 11% were vertebrates. For both pellets and prey remains, the main prey were orthopterans, with 70.5% in the pellets and 56.4% in prey remains (Table 3). Those values compared favorably with our observations of prey deliveries at the nest, in which arthropods accounted for 71.4% of prey delivered. Arthropods have been reported as the most common prey item in the American Kestrel's diet during the summer in the semiarid forest of Argentina (Sarasola et al. 2003) and in Georgia, U.S.A. (Parrish 2007). In contrast, American Kestrels in Canada were not observed delivering insects to their young; instead, small mammals comprised 73.7% of vertebrate prey deliveries to nests (Gard and Bird 1990).

Our study provides new information about the American Kestrel in Argentina, where it has been little studied. More extensive studies on populations of kestrels ranging throughout southern South America are needed to determine how variation in factors such as abundance and availability of prey and weather may affect prey delivery rates and parental care, and ultimately, reproductive success of kestrels in this region.

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Table 3. Diet of nestling American Kestrels (*Falco sparverius*) in semiarid forest in Parque Luro Reserve, central Argentina, determined by pellet analysis, prey remains analysis and focal observations (N = Number of Prey and F = Frequency).

Prey Type	Pellets		PREY REMAINS		OBSERVATIONS	
	N	F (%)	Ν	F(%)	Ν	F(%)
Vertebrates						
Rodents	5	4.3	19	2.3	-	-
Birds	21	18.0	59	7.0	-	-
Reptiles	8	6.8	16	1.9	-	-
Subtotal vertebrates	34	29.1	94	11.2	31	17.7
Arthropods						
Orthoptera	66	56.4	592	70.5	-	-
Homoptera	4	3.4	59	7.0	-	-
Diptera	-	-	1	0.1	-	-
Hymenoptera	1	0.9	22	2.6	-	-
Coleoptera	8	6.8	49	5.8	-	-
Mantodea	4	3.4	17	2.0	-	-
Araneae	-	-	1	0.1	-	-
Scorpionida	-	-	5	0.6	-	-
Subtotal arthropods	83	70.9	746	88.8	125	71.4
Unidentified prey	-	-	-	-	19	10.8
Total number of prey items	117		840		175	

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