

BREEDING BEHAVIOR OF AMERICAN KESTRELS RAISING MANIPULATED BROOD SIZES IN YEARS OF VARYING PREY ABUNDANCE

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ABSTRACT.—Behavioral responses of American Kestrels (*Falco sparverius*) to manipulated broods of two, five, and seven young were studied in southwestern Quebec during 1986 and 1987. Average territory size was inversely correlated with small mammal abundance which differed significantly between years, but was not influenced by brood size in either year. Parents of all three brood sizes devoted less time to searching for food, and more time to resting and maintenance behavior in 1987 than 1986. Interannual differences in hunting behavior were attributable to variations in the percent time spent perch-hunting. Hover-hunting times were similar between years and among brood sizes. Despite less time spent hunting, rates of prey capture and food delivery to the nest were significantly higher in 1987. Received 25 July 1989, accepted 15 Feb. 1990.

According to Lack's (1954, 1968) hypothesis, the observed average brood size should produce the greatest number of young surviving to fledging. Studies in which brood size has been experimentally enlarged have more often than not refuted Lack's theory by finding the most productive brood size to be larger than the average brood size (Martin 1987). Reproductive success in one breeding season represents only a portion of the total lifetime output for an iteroparous species. Increasing reproductive success at any one breeding attempt may require a greater expenditure of reproductive effort by the parents resulting in a decreased probability of survival to the next breeding attempt. Therefore, individuals may raise broods smaller than the most productive size to maximize lifetime reproductive output (Williams 1966, Charnov and Krebs 1974).

Differential parental mortality in relation to brood size is difficult to detect since low recovery rates of banded individuals necessitate large sample sizes to demonstrate the existence of significant differences (DeSteven 1980, Nur 1984a). Monitoring parental weight changes during the breeding season can provide an indirect measure of the cost of reproduction, although the relationship of parental weight loss to post-reproductive survival is unclear (Martin 1987, but see Nur 1984a). Furthermore, weight loss during breeding has been suggested to be an adaptation which lessens the energetic expenditure associated with heightened feeding activity (Freed 1981, Norberg 1981).

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Reproductive effort can also be estimated indirectly by observing parental behavior and rates of food provisioning to the young in relation to variation in brood size. Subsequent adult survival cannot be ascertained by this procedure, but it can indicate whether parents respond to changes in brood size by modifying foraging costs, or whether they are near the limit of their reproductive capabilities as Lack (1954, 1968) suggested. We report here on the influence of experimental manipulation of brood size on parental behavior and feeding frequency in the American Kestrel (*Falco sparverius*).

METHODS

This study was performed from April to July 1986 and 1987 in southwestern Quebec. We used a population of wild kestrels breeding in nestboxes erected by the Macdonald Raptor Research Centre in the western region of the island of Montreal, Ile Perrot and eastern Vaudreuil-Soulanges County. Nestboxes were placed on hardwood trees or snags located in hedgerows bordering abandoned agricultural fields.

Breeding records for the wild population for the four previous years indicated that broods of five produced, on average, the greatest number of young surviving to fledging (unpubl. data). We manipulated broods of five to create small and large broods of two and seven young, respectively. Manipulations were always performed within two days of the hatching of the last young. To minimize age and weight differences, we only transferred chicks between nests in which young had hatched within one day of each other.

Parental behavior was recorded during 2-h observation periods. Observations were taken from partially concealed positions about 50–100 m from the nestboxes, and were performed throughout the nestling period. Observation sessions were early morning (07:00–11:00 EST) and late afternoon (15:00–17:30), as birds were usually inactive around midday (pers. obs.). To eliminate bias due to pre-fledging mortality, we only observed nests where all the young were present. Data from all nests of equivalent original brood size were pooled for statistical analysis. Behavioral observations were recorded using a raptor actigram, an ethogram with alphanumeric notations (Walter 1983). The duration of each behavior was recorded and the behavior was classified into one of five categories: hunting, perched, maintenance, caring for the young, and interspecific behavior. Hunting included periods of flapping or soaring flight interspersed with bouts of hover-hunting. Perch-hunting, where birds were observed continually moving their heads and scanning the surroundings, was also included in this category. The latter was differentiated from perched (or resting) behavior where kestrels perched but were not alertly monitoring their territory. Direct flight between perches was also included with perched behavior. Maintenance activities included feeding, preening, or scratching sessions. Caring for the young (brooding or feeding) could not be observed directly, but was inferred from time parents spent in their nestbox. Percentage time data were transformed with an arcsin square root transformation prior to statistical analysis (Sokal and Rohlf 1981). In conjunction with behavioral observations, we recorded rates of prey capture and the number of food deliveries to the nest. Prey capture rates were determined either directly by viewing kestrels diving into the vegetation and emerging with prey, or indirectly by observing kestrels returning to a perch in possession of prey after having previously flown off without a prey item.

To determine relative prey abundance, snap-trapping for small mammals was performed at active nests. Trapping was done near locations where kestrels were observed hunting, and in similar habitats. At each site, 36 Victor snap traps, baited with peanut butter and

rolled oats, were laid out 5 m apart in a 6 × 6 grid arrangement. Traps were checked each morning for ten consecutive days. At least four times during the nestling period, sweep-net samples were collected near active nests to monitor the abundance of grasshoppers, often a major prey item of American Kestrels (Palmer 1988). However, samples were only assessed qualitatively to determine when peak abundance occurred.

The sizes of breeding territories were determined with a spot-mapping technique. The location of kestrels in relation to geographic landmarks such as buildings, roads, hedgerows, or dead snags was marked on acetate overlays of 1:15,000 scale aerial photographs. To compensate for variations in altitude on the photographs, the exact scale was determined by a photo scale reciprocal formula based on ground distances derived from a 1:20,000 scale topographical map (Avery and Berlin 1985). Using a minimum of 20 mapped points, territories were considered as the maximum polygon area created by connecting the outermost locations to form a convex polygon (Odum and Kuenzler 1955). Area of the territory was measured using a dot-grid technique (Avery and Berlin 1985).

All statistical tests followed procedures from Sokal and Rohlf (1981). Reported values are mean ± one SD.

RESULTS

Kestrels maintained smaller breeding territories in 1987 than in 1986. Parents of all three brood sizes displayed this trend, with differences between years being significant for parents raising broods of two or five young (Table 1). However, within each year there was no significant difference in territory size corresponding with variations in brood size (Kruskal-Wallis test, $P > 0.25$ for both years). In 1987 there was a trend for territories to be larger with increasing brood size. This may have been significant if sample sizes were larger.

Average small mammal abundance, as estimated by snap-trapping, was 3.84 ± 4.03 mammals/100 trap nights in 1986 ($N = 10$ trap sites), and 38.23 ± 23.15 mammals/100 trap nights in 1987 ($N = 7$ trap sites). The difference between years was highly significant (Mann-Whitney test, $U = 7$, $P < 0.01$). Meadow voles (*Microtus pennsylvanicus*) constituted the greatest proportion of mammals caught in both years: 68.9% in 1986 (106 mammals total caught), and 97.1% in 1987 (725 mammals total caught). Shrews (*Sorex cinereus* and *Blarina brevicauda*) composed 22.6% of the total in 1986 and 1.9% in 1987. Deer mice (*Peromyscus maniculatus*) formed the remainder in both years. Territory size was negatively correlated with estimates of local small mammal abundance (Spearman's $r = -0.770$, $N = 17$, $P < 0.005$; Fig. 1).

Although sample sizes are too small to permit intra-annual comparisons of prey density in relation to brood size, the general trend of increased mammal abundance in 1987 likely applies at all breeding territories. In both years of this study, several trapping sites were situated between two neighboring nests with different brood sizes. Qualitatively, vegetative structure in these breeding territories and at the trap site appeared similar,

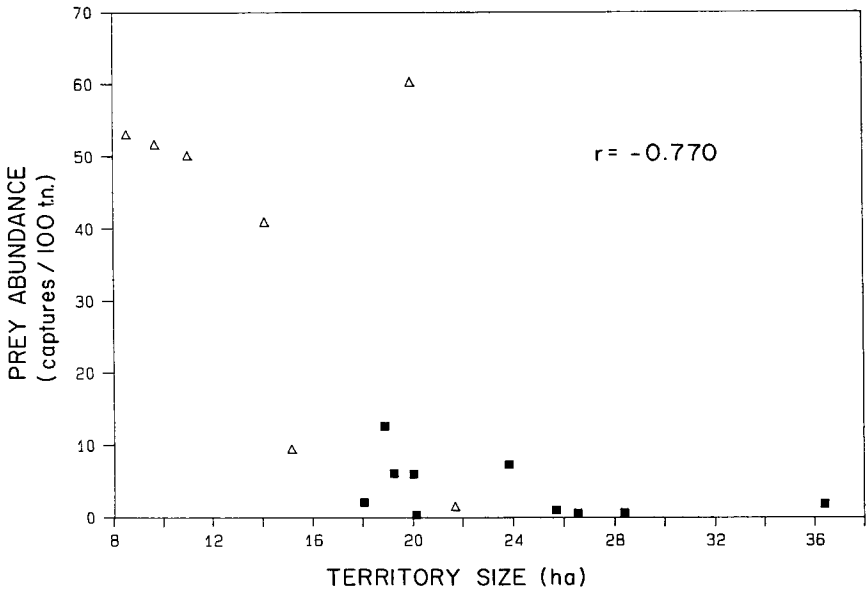


FIG. 1. Territory size of American Kestrels in relation to relative small mammal abundance (captures/100 trap nights). Squares = 1986 territories; triangles = 1987 territories.

so mammal abundance at the trap site probably reflects a reasonable estimate of prey availability at all nearby sites.

Climatic factors were similar during breeding periods in both years. In the region of the study area, total precipitation during the nestling stage in 1986 (1 May to 30 June) was 198.2 mm and average temperature was 14.9°C. In 1987 the nestling stage spanned from 1 May to 6 July, and in that period total precipitation was 192.0 mm and average temperature

TABLE 1
SIZE OF BREEDING TERRITORIES (HECTARES) OF AMERICAN KESTRELS IN 1986 AND 1987 IN
RELATION TO BROOD SIZES ESTABLISHED BY EXPERIMENTAL MANIPULATION

Brood size	1986		1987	
	N	$\bar{x} \pm SD$	N	$\bar{x} \pm SD$
2	7	21.3 \pm 4.0	5	11.3 \pm 2.1 ^a
5	4	27.6 \pm 7.6	6	12.4 \pm 2.9 ^b
7	5	22.5 \pm 5.0	4	16.3 \pm 5.9
Pooled	16	23.2 \pm 5.6	15	13.1 \pm 4.0 ^a

^a $P < 0.01$; ^b $P < 0.05$, Mann-Whitney *U*-test, for differences between years.

TABLE 2
TIME-ACTIVITY BUDGETS FOR AMERICAN KESTRELS REARING VARIOUS SIZED BROODS
ESTABLISHED BY EXPERIMENTAL MANIPULATION

Brood size	Sex	Year	Hunting			Perched	Maintenance	Care of young
			Hover	Perch	Total			
2	M	1986	3.3	71.2 ^b	74.1 ^b	21.0	4.4 ^b	0.1
		1987	5.7	42.4	50.1	39.0	12.6	0.1
	F	1986	4.5	44.5 ^b	49.0 ^a	25.7 ^a	3.0	21.7
		1987	3.9	15.5	19.4	53.8	7.6	18.7
5	M	1986	3.4	79.5	82.9	15.0	2.0	0
		1987	3.7	61.8	65.5	29.1	4.8	0.6
	F	1986	4.3	39.2	43.5	38.2	3.2	14.8
		1987	2.1	34.8	36.9	46.0	4.5	12.7
7	M	1986	3.6	78.3 ^b	81.9	17.2	0.8 ^b	0
		1987	2.8	68.0	70.8	22.8	5.5	0.7
	F	1986	2.2	63.2 ^a	65.4 ^a	16.7 ^a	2.7	14.2
		1987	4.6	27.0	31.6	50.0	2.7	15.3

Values that differ significantly between years for each activity are noted as ^a $P < 0.01$; ^b $P < 0.05$, Mann-Whitney U -test.

was 15.8°C (Environment Canada 1986, 1987). Weather has been shown to explain only a minor proportion of variation in small rodent activity (Vickery and Bider 1981), therefore differences in trapping success between years likely reflect actual interseasonal variations in prey abundance and not changes in behavioral patterns produced by environmental conditions.

We observed parent birds for 77.7 h in 1986 and 60.6 h in 1987. Time activity budgets revealed that parents of all brood sizes devoted less time to hunting in 1987 than in 1986 (Table 2). Differences were significant for parents with broods of two, and for females with broods of seven (Mann-Whitney U -test, $P < 0.05$). For males rearing broods of seven, the difference approached significance ($P = 0.051$). The percent of total time parents spent hunting from flight was not significantly different between years for any brood size. Therefore, decreases in total hunting time were primarily a result of less time spent perch-hunting. Within each year, the total time spent hunting did not differ significantly among brood sizes for either sex (Kruskal-Wallis test, $P > 0.10$ in all four cases). Although males of all brood sizes spent more time hunting than females, these differences were only significant for broods of two and five in 1986 and broods of seven in 1987 (Mann-Whitney U -test, $P < 0.05$ in all three cases). Kestrels responded to decreased hunting time in 1987 by allotting more time to resting or maintenance activities (Table 2). Parents of all

TABLE 3
CAPTURE RATES FOR VERTEBRATE PREY AND DELIVERY RATES TO THE NEST BY AMERICAN KESTRELS RAISING VARIOUS-SIZED BROODS ($\bar{x} \pm SD$) IN 1986 AND 1987

	Brood size	1986	1987
Prey capture (prey items/h)	2	0.51 \pm 0.41	1.37 \pm 0.95 ^b
	5	0.44 \pm 0.73	0.88 \pm 1.20
	7	0.26 \pm 0.39	0.99 \pm 0.80 ^a
	Pooled	0.41 \pm 0.49	1.03 \pm 0.96 ^a
Prey delivery (prey items/h)	2	0.33 \pm 0.56	0.58 \pm 0.47
	5	0.25 \pm 0.38	0.45 \pm 0.69
	7	0.18 \pm 0.29	0.91 \pm 0.77 ^a
	Pooled	0.26 \pm 0.43	0.70 \pm 0.70 ^a

^a $P < 0.01$; ^b $P < 0.05$, Mann-Whitney U -test, for differences between years.

brood sizes spent more time involved in these behavioral patterns in 1987 than in 1986. Differences between years were generally not significant, although females raising two and seven young spent significantly more time at rest in 1987 than in 1986 (Mann-Whitney U -test, $P < 0.01$). Females usually spent more time perched than males, but differences were only significant for broods of five in 1986 and broods of seven in 1987 (Mann-Whitney U -test, $P < 0.05$).

For all brood sizes, females spent similar amounts of time brooding and feeding young as inferred from time spent in the nestbox (Table 2). Early in the nestling stage females probably devoted most of their time to brooding young until they were able to maintain effective thermoregulation (Dunn 1979). Later, when young grew too large to brood, time spent in the nestbox probably reflects bouts of feeding. Males spent almost no time in direct care of the young.

Agonistic interactions with other birds, which accounted for less than 0.5% of the total activity budget, have been omitted from the following discussion.

A comparison of all breeding pairs, independent of brood size, revealed that the capture rate for vertebrate prey was over twice as high in 1987 than in 1986 (Table 3). Parents of all brood sizes had greater hunting success in 1987 as compared with 1986, with differences being significant for parents raising broods of two and seven. Within each year however, there was no significant difference in hunting success among brood sizes (Kruskal-Wallis test, $P > 0.15$ in 1986, $P > 0.25$ in 1987).

The proportion of invertebrates to vertebrates in total prey captures was not known, but sweep-net surveys suggested that grasshopper and

cricket abundance during the nestling period was low. Peak invertebrate abundance did not appear to occur until after the young had fledged. Seasonal dietary changes from vertebrate to arthropod prey (Balgooyen 1976, Phelan and Robertson 1978) may have occurred at this time. Insects probably did not constitute a major part of the diet of parents during the nestling period. Parents were not observed delivering insects to the young.

Trends in the rate of vertebrate prey deliveries to young paralleled those observed for prey capture rates (Table 3). Small mammals formed 73.7% of the total vertebrate prey deliveries in 1986 and 78.7% in 1987. These values likely underestimate the true proportion, as it was not always possible to make a positive identification of the prey item delivered. Unidentified prey made up 15.8% of all deliveries in 1986 and 19.1% in 1987; some of these were probably small rodents. Birds and snakes accounted for the remainder of the prey items in both years. For all brood sizes, parents provided young with more prey per hour in 1987 than in 1986, although a significant increase was noted only for broods of seven in 1987 (Table 3). Within each year, the rate of food delivery was not related to brood size (Kruskal-Wallis test, $P > 0.50$ in 1986, $P > 0.10$ in 1987).

DISCUSSION

Territory size of breeding American Kestrels varied inversely with small rodent density. Differences in average territory size between years in response to changes in prey density would appear to support the hypothesis that kestrels are directly monitoring prey abundance and adjusting breeding territory size accordingly. This is supported by a previous study (Bowman and Bird 1986) at the same site that reported a similar inverse relationship between prey abundance and kestrel territory size. Microtine rodent abundance in the earlier study was similar to our estimates for 1986, and territory sizes during these two periods were nearly identical (24 ± 4 ha, Bowman and Bird (1986); 23.2 ± 5.6 ha, this study for 1986). Alternatively, although not examined, territories might have been established based on vegetative structural features correlated with expected prey abundance (Smith and Shugart 1987). The extent of the foraging area did not vary significantly in response to changes in energetic demands associated with differences in brood size. Kestrels may not alter territorial boundaries once established, particularly if the original territory maximizes rates of prey capture while minimizing costs associated with territorial defense. In 1987 birds raising seven young tended to have slightly larger territories compared with other brood sizes, but rates of prey capture were similar. Therefore, an increase in territory size does not appear to improve hunting success.

The significantly lower feeding rates of young by parents in 1986 are probably attributable to reduced prey abundance in that year relative to 1987. Pre-fledging mortality from starvation was high for broods of five and seven in 1986 (Gard 1989), indicating that parents were unable to adequately feed average and enlarged broods.

Prey densities were much higher in 1987 than in 1986. While parents with broods of two and five spent less time hunting in 1987 than in 1986, their rates of prey capture were much higher. Decreased hunting time suggests that because of greater prey abundance and enhanced hunting success in 1987, kestrels could capture sufficient food to meet nestling and adult requirements in a shorter span of time than in 1986. Parents rearing seven young also spent less time hunting in 1987, and had significantly higher prey delivery rates than in 1986. Total time spent hunting by parents with five or seven young was, however, similar in 1987. Parents rearing seven young made more prey deliveries than parents with smaller broods, although the increase was not significant. Several pairs of kestrels were capable of raising all young in a brood of seven to fledging in 1987, but these young fledged significantly lighter than young in broods of five (Gard 1989). This may have resulted in higher post-fledging mortality, as evidence from other studies indicates that post-fledging survival is correlated with fledging weight (see Martin 1987). Variations in prey abundance suggest that kestrels were not always food limited, and that the inability to rear young in enlarged broods to normal fledging weights in 1987 may have been due to adaptive limitations upon parental feeding behavior as proposed by Hussell (1972) and Nur (1984b). As Hussell (1972) noted, other activities (e.g., rest, maintenance) also have a selective value in terms of maximizing lifetime reproductive output. Therefore, amount of food brought to the young may be limited not by the environmental food supply, but by a behavioral component which restricts the amount of time parents spend food gathering irrespective of brood size.

Hover-hunting never accounted for more than 20% of the total time spent hunting, a ratio corresponding with values reported in other studies (Balgooen 1976, Rudolph 1982, Toland 1987). The proportion of time spent hover-hunting was larger in 1987 than 1986 due to the relatively greater use of perch-hunting in 1986 than in 1987. This is in accord with theoretical models which predict switching to energetically less expensive hunting methods when prey abundance declines (e.g., Norberg 1977). Since the percentage of the total daily activity budget spent hover-hunting does not vary between years or brood sizes, this activity may represent an energetic ceiling on parental performance (Drent and Daan 1980). Hover-hunting has been found to yield higher rates of prey capture and

gross energy intake than perch-hunting. However, energetic consumption during hovering and forward flight is estimated to be about seven times greater than while at rest (Rudolph 1982).

Habitat physiography can be a contributing factor. Toland (1987) noted that kestrels in Missouri favored foraging in mowed or grazed pastures where they hunted primarily from perches. When birds hunted in undisturbed, tall grass meadows a significant increase in hover-hunting was noted, with this strategy comprising 27% of total hunting time. High vegetation in fallow fields made prey detection from perches more difficult. In this habitat, kestrels presumably were compelled to spend more time hover-hunting to maximize prey detection and capture rates despite the higher energetic costs associated with this hunting method. In our study, most territories were in undisturbed fields where vegetational height increased throughout the breeding season. Kestrels may have maximized the time spent hover-hunting in order to capture sufficient prey to meet nutritional demands. The lack of difference in hover-hunting time among brood sizes or years is consistent with the hypothesis that kestrels were at an energetic ceiling for this activity. For parents raising enlarged broods, increasing time engaged in hover-hunting behavior may have incurred physiological costs which outweigh benefits expressed as increased prey capture rates and hence, increased offspring feeding rates (Nur 1984b).

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