Influence of brood-size manipulation on nestling growth, fledging success and parental behaviour in American Kestrels

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ABSTRACT

M.Sc. N. Gard Renewable Resources (Wildlife)

INFLUENCE OF BROOD-SIZE MANIPULATION ON NESTLING GROWTH, FLEDGING SUCCESS AND PARENTAL BEHAVIOUR IN AMERICAN KESTRELS

Brood size was manipulated in captive and wild American Kestrels (Falco sparverius) during 1986 and 1987. Broods of 2, 5 (the largest naturally occurring brood size), and 7 were established. Wild nests had higher fledging success in 1987 than 1986 for all brood sizes. Generally, broods of 5 and 7 had significantly more young fledging than broods of 2, while the number of young fledging from these two larger brood sizes did not differ significantly.

In nests without pre-fledging mortality, growth rate, tarsal and antebrachial length were not influenced by brood size. Young in enlarged wild broods fledged significantly lighter than young from other broods.

Interannual differences in fledging success for wild nests corresponded with variations in vertebrate prey density. Parents of all brood sizes hunted less in 1987 than 1986, but had higher prey capture and nestling feeding rates.

This study suggests that the naturally occurring brood size is the largest which kestrels can, on average, feed without lowering nestling quality.

RESUME

INFLUENCE DE LA MANIPULATION DES COUVEES DE CRECERELLE D'AMERIQUE SUR LA CROISSANCE, LA SURVIE ET LES SOINS PARENTAUX DES OISILLONS

Le volume de couvée de Crécerelle d'Amérique (Falco sparverius) en captivité et en liberté fut manipulé durant les années 1986 et 1987. Des couvées de 2, 5 (la plus grosse couvée chez les populations naturelles) et 7 oisillons furent établi. En règle générale, les novices de 5 ou 7 oisillons si on compare aux couvées de 2 oisillons, mais le nombre de novices entre les grosses couvées ne démontraient aucune différence significative.

Les taux de croissance, les longs tarsiaux et antibranchiaux chez les oisillons ayant survécu la période de pre-novice ne démontraient aucune influence dû au volume de couvée. Chez la population naturelle de Crécerelle, les oisillons présents dans les couvées de volume plus important, 5 ou 7 oisillons, pesaient significativement moins que les autres couvées.

La différence inter-annuelle de survie des oisillons correspondait à la densité de la population des proies. Les parents des couvées chassaient moins en 1987 mais démontraient un taux plus élevé de capture de proie et d'alimentation des oisillons.

Cette étude suggère que la couvée naturelle de la Crécerelle est le plus grand volume que celles-ci peuvent nourrir en moyenne.

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PREFACE

Clutch size represents one of the most important life-history parameters. Lack (1954) hypothesized that clutch size in nidicolous birds has evolved by natural selection toward a size corresponding with the greatest number of young for which parents can find food. Lack's hypothesis has been extensively tested for passerines and seabirds in studies where brood size has been experimentally augmented and the effect on growth and fledging success of the young examined. Lack's hypothesis has been supported in about a third of these experiments, while the others found that the clutch size laid was smaller than the most productive brood size (reviewed by Lessells 1986, Martin 1987).

The validity of Lack's hypothesis to raptors has not been widely tested. Although a detailed experiment has been performed on owls (Korpimaki 1987), studies on diurnal raptors have usually involved manipulating brood size at only a very small number of nests (e.g. Cavé 1968, Balgooyen 1976).

The American Kestrel (Falco sparverius), probably the most numerous of North American falconiformes (Palmer 1988), is a suitable raptorial species on which to perform a detailed brood manipulation experiment. The objectives of this study were to examine growth and fledging success of nestlings and behavioural responses of parents following experimental manipulation of brood size. This study should improve our understanding of factors that affect clutch size and breeding success in raptors.

As permitted by the Faculty of Graduate Studies, this thesis includes the texts of two manuscripts to be submitted to journals for publication. The first, presented in Chapter 1, describing growth and fledging success of nestlings will be submitted to the "Journal of Animal Ecology". The second, presented in Chapter 2, discussing behavioural responses of parents will be submitted to "The Wilson Bulletin". Both manuscripts will have Dr. D. M. Bird as co-author. Data collection and analyses were conducted independently by the senior author. References, tables, and figures appear after the manuscript in which they are cited and the style adopted for each chapter is that of the journal to which the manuscript will be submitted.

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The following is included in accordance with the regulations of the McGill University Faculty of Graduate Studies:

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CHAPTER 1

NESTLING GROWTH AND FLEDGING SUCCESS IN MANIPULATED AMERICAN KESTREL BROODS

SUMMARY

1) Brood manipulation experiments were performed on captive and wild American kestrels (Falco sparverius) in southwestern Quebec during 1986 and 1987.

2) A nest of five young was considered the largest normally occurring brood size, and manipulations enlarged or decreased broods to 7 or 2 young, respectively.

3) Enlarged broods had slightly, but not significantly higher fledging success than normal sized broods. Significantly more young fledged from broods of 5 and 7 than from broods of 2 for captive nests and for wild nests in 1987.

4) In manipulated broods where no pre-fledging mortality occurred, brood enlargement significantly lowered fledging weights of wild, but not captive birds. Brood manipulation had no effect on either rate of weight gain or length of the tarsus or antebrachium. Development of the ninth primary feather was slower in enlarged wild broods.

5) Membership within a specific brood had a significant influence on fledging weight and growth rate of females and on bone length for both sexes.

INTRODUCTION

Lack's (1954, 1968) hypothesis regarding the evolution of clutch size in nidicolous birds explicitly stated that clutch size, and hence brood size, is regulated by food availability. Therefore, given the prevailing food supply, the mean clutch size of a population should produce, on average, the greatest number of offspring surviving to breed. If the ability of parents to feed the young limits brood size, then nestlings in larger than average sized broods should be less well-nourished, and consequently at a comparative disadvantage compared with young in smaller broods.

Naturally occurring variations in clutch size among individuals within a population may reflect differences in the reproductive ability of parents. Older, experienced breeders may be more adept at finding food and consequently, able to successfully rear more young than first-time breeders (Perrins and Moss 1974, Newton 1976). Manipulation of brood size is therefore the most appropriate method of testing Lack's hypothesis, as this removes any effect of correlation of parental ability and brood size (Martin 1987). Many such manipulation experiments have been performed, primarily using seabirds or passerines. Results from these studies have been conflicting; about a third support Lack's hypothesis, while the others found that more young fledged from clutches larger than the clutch size laid (Martin 1987). Reducing clutch size below the most productive size is considered a means of maximizing lifetime reproductive output (Williams 1966, Charnov and Krebs 1974). As Askenmo (1977) noted, the variability of results limits the ability to generalize from such experiments to other taxonomic groups, suggesting that each species needs to be investigated separately.

Several studies on raptors have observed differences in reproductive success due to naturally occurring variation in brood size (e.g. Cavé 1968, Moss 1979, Korpimaki 1987). However, little work has been performed to study reproductive success in manipulated broods. Using only 2 nests, Balgooyen (1976) found no effect of increased brood size on fledging success or weight for American kestrels (Falco sparverius). Korpimaki (1987) reported that more young fledged from augmented Tengmalm's owl (Aegolius funereus) broods than normal sized broods, but young from enlarged broods weighed less at fledging. Newton (1979) remarked that in many aspects of their breeding strategies small raptors resemble passerines while larger species are similar to seabirds. Due to this similarity in reproductive strategies, brood manipulations on raptorial species may be instructive for comparison with these other two groups which have been used extensively in manipulation experiments.

Here I report on nestling growth and fledging success in manipulated broods of the American kestrel. If Lack's hypothesis applies to this species, and brood size is indeed regulated by food availability, I predicted that experimentally increasing brood size should lead to 1) decreased fledging success, 2) decreased nestling weight at fledging and 3) slower growth rates when compared with naturally occurring, average sized broods. Experimentally reduced broods were studied to determine whether growth rates and fledging weights of young from these broods are similar to those of young in average sized broods, as would be predicted from Lack's hypothesis. While young in average sized broods may be well-nourished, this does not necessarily imply that they are growing at their physiological limit (Martin 1987). Since altricial young rely on parents for food, the rate at which they are fed may be constrained by other demands on the parent such as time spent acquiring food. To test this, manipulation experiments were also performed with captive American kestrels.

In captivity, birds are provided food ad libitum, thus minimizing food acquisition time while providing parents the opportunity to feed young to satiation. Assuming wild young in normal sized broods are well-fed, I predicted that fledging success, weights at fledging and growth rates for young in small and normal sized broods would be similar for captive and wild kestrels. However, captive birds should be capable of successfully keeping all young in augmented broods adequately nourished. Therefore, I predicted that enlarged broods in captivity would display higher fledging success and better nestling growth performance than enlarged broods in the wild.

METHODS

Study areas- This study was performed from April to August in 1986 and 1987. The study used a population of wild kestrels located in the western region of the island of Montreal, Ile Perrot and the eastern region of Vaudreuil-Soulanges county (45° 25' N, 74° 05' W) in southwestern Quebec. All breeding pairs used in this study bred in nestboxes erected by the Macdonald Raptor Research Centre (MRRC). Nestboxes were placed on hardwood trees or snags located in hedgerows bordering fallow agricultural fields. Dimensions of all nestboxes were identical (22.9 x 25.4 x 27.9 cm).

Captive studies used kestrels from the MRRC pedigreed colony. Pairs were housed in 2.4 x 1.2 x 2.4 m high plywood enclosures under natural photoperiod. Each pen was equipped with a one-way glass observation window to view the interior of the cage and nestbox. All captive pairs were fed ad libitum on day-old cockerels supplemented with a vitamin/mineral mix (SA-37, Rogar STB, Montreal Quebec).

Manipulations- Records maintained by the MRRC from 1982 to 1985 for nestboxes in the wild indicated that the largest, and most common, clutch size was 5 eggs (45 of 61 active nests). Modal clutch in captivity was also 5 eggs. Therefore, for this study broods of 5 were considered to produce, on average, the greatest number of young. Manipulations were performed to increase or decrease brood sizes to 7 and 2 young, respectively. Manipulations were always performed within 2 days of the hatching of the last young. To minimize age and weight differences among the young, transfers were only done between nests in which the young had hatched within 1 calendar day of each other. For wild nests, young were usually transferred from other wild nests. In several cases this was not possible, and young from the captive breeding colony were fostered into these nests to augment brood size. Nests from which young were taken formed the experimental group of reduced broods. If surplus young remained after manipulations were performed on wild nests, they were removed to the MRRC, hand-reared and released at the end of the breeding season. Thirty-four wild nests (18 in 1986, 16 in 1987) and 28 captive nests were used in this study.

Measurements- At 5-day intervals from hatching to fledging, young from all captive and wild nests were weighed to the nearest gram with a 300 gm Pesola scale. Length of the tarsus, antebrachium and ninth primary were measured to the nearest 0.1 mm with vernier calipers following the procedures described by Olendorff (1972). All young were measured by NWG, except for captive young in 1986 which were measured by an assistant. Morphological measurements were always taken on the left side of the body. All measurements were taken between 1100 and 1300 hours. Amount of food in the crop was assessed qualitatively at each weighing. Chicks were rarely observed with fully distended crops, and undigested food probably contributed little to the total weight. To differentiate between nestlings, all birds were distinctively marked with waterfast colour markers until they were old enough to be fitted with U.S. Fish and Wildlife Service bands. Sex of the young was known prior to fledging on the basis of dimorphism in plumage colouration.

Statistical Analyses- Kestrels exhibit reversed size dimorphism as is standard among raptors (Newton 1979), with females being approximately 15% larger than males (Palmer 1988). Therefore, fledging weights and growth rates of each sex were analyzed separately. Asymptotic weights and growth rates were determined by Ricklefs' (1967) graphical method, using the logistic growth equation. This method involves the use of conversion factors to transform sigmoidal growth curves into linear functions. The slope of the resulting line is proportional to the growth rate constant, K.

Tarsal and antebrachial length reached stable values about 5-7 days prior to fledging. These asymptotic values were used for statistical comparisons among groups. Balgooyen (1976) indicated that tarsal measurements do not reflect the degree of sexual dimorphism of body size, which is likely since both sexes take similar prey. Therefore, for all brood sizes, morphological measurements for both sexes were pooled, after verifying that differences between sexes were not significant.

To determine whether significant differences existed among brood sizes for weight, growth rate, tarsal or antebrachial length, single classification analyses of variance were performed for each parameter, based on all young surviving to fledging age in the study. However, since pre-fledging mortality may influence subsequent growth of the remaining young within a brood, I also performed separate analyses using only nests where no pre-fledging mortality occurred. For these nests, two-level nested analysis of variance was used to determine whether significant differences existed between brood sizes or among broods of a specific size for all 4 growth parameters. Pairwise t-tests were used to locate significant differences among groups. For primary length, only differences between brood sizes were examined. All statistical procedures followed Sokal and Rohlf (1981). Reported values are mean ± 1 SD.

RESULTS

Clutch initiation and size- Dates of clutch initiation were converted to integer values based on the number of julian days after 1 April when the first egg was laid. Clutch initiation dates ranged from 10 April to 5 May in 1986 ($\bar{x}$ = 23.8, n = 18) and 8 April to 11 May in 1987 ($\bar{x}$ = 21.4, n = 16). There was no significant difference in the median date of clutch initiation between years ($t = 0.88$, $p > 0.05$). Mean clutch size of all active nests was 4.8 ± 0.4 eggs in 1986 and 4.7 ± 0.5 eggs in 1987. The difference between years was not significant ($t = 0.81$, $p > 0.05$).

Fledging success- Productivity of wild nests was higher in 1987 than in 1986 for all 3 brood sizes, and significantly so for broods of 5 and 7 (Table 1). In 1986, the average number of young fledging per brood did not differ significantly among the 3 brood sizes (Kruskal-Wallis test, $H = 2.08$, $p > 0.25$). Significantly more young fledged from broods of 5 and 7 than broods of 2 in 1987 ($H = 17.07$, $p < 0.001$). The percentage of nests from which at least one young fledged in 1986 was 71, 80, and 33 for broods of 2, 5, and 7, respectively. In 1987, all nests of all brood sizes had at least one young fledging (Appendix). Breeding records for the same wild population from 1983 to 1985 indicate that over that time period, average productivity per brood of 5 was 4.67 ± 0.50 young (n = 9, unpubl. data). This was significantly higher than for broods of 5 in 1986 ($\bar{x}$ = 1.80, Mann-Whitney test, $U = 0$, $p < 0.001$), but not significantly lower than productivity from broods of 5 in 1987 ($\bar{x} = 5.00$, $U = 21$, $p > 0.05$).

Variations in fledging success between years for captive broods were not significant (Mann Whitney U test, $p > 0.05$ for all 3 comparisons), thus data were pooled. As with wild nests in 1987, broods of 5 and 7 had significantly higher average fledging success than broods of 2 ($H = 13.79$, $p < 0.01$), but were not significantly different from each other (Table 1). The number of young fledged from wild broods in 1987 was not significantly different than for similar sized captive broods (Mann-Whitney U test, $p > 0.05$ for all 3 comparisons), but was lower for wild broods of 5 and 7 in 1986 (Mann-Whitney U test, $p < 0.05$ for both comparisons).

In experimentally enlarged broods, fledging success was independent of parentage, with 63% of natural young and 62% of fostered young fledging ($G = 0.015$, $p > 0.9$).

Weight and growth rates- Since kestrels raised in captivity exhibited no significant variation in fledging weight between years (t-test, $p > 0.05$ for all 3 brood sizes for each sex), data were pooled. Analyses were therefore based on 9 experimental groups: captive nests, and 1986 and 1987 wild nests, each with 3 brood sizes.

Variances in asymptotic weights between groups were homogeneous for both sexes (F-test for equality of variances, $p > 0.05$). One-way analyses of variance based on all young surviving to fledging indicated that highly significant ($F_{8,97} = 8.20$, $p < 0.005$ for males, $F_{8,89} = 7.75$, $p < 0.005$ for females) differences existed in fledging weights among brood sizes for both sexes (Table 2a,b).

Manipulation of brood size had no effect on fledging weights of captive bred young. For wild birds, young from small and normal sized broods generally fledged at weights equal to captive-reared young. Only females from wild broods of 5 in 1986 were significantly lighter at fledging than their captive counterparts.

Fledging weights of young from augmented wild broods varied between years. In 1986, young from broods of 7 fledged at weights similar to young in smaller sized broods. However, heavy pre-fledging mortality in these broods of 7 likely led to a significant reduction in competition for food among the surviving young. In 1987, although fledging success from broods of 7 was high, young were significantly lighter at fledging than chicks in broods of 2 and 5.

Variances in growth rate constants between groups were homogeneous for males ($F = 27.73$, $p > 0.05$), but heterogeneous for females ($F = 231.04$, $p < 0.05$). The heterogeneity results from the small degree of variation among young from wild broods of 7 in 1986. However, this group was retained in the analysis of variance because moderate heterogeneity of variance has no serious effect on the overall test of significance (Sokal and Rohlf 1981).

Although growth rates for males differed among groups (Table 2a), one-way analysis of variance indicated that these differences were insignificant ($F_{8,97} = 1.90$, $p > 0.05$). Growth rates of female young differed significantly among experimental groups ($F_{8,89} = 5.45$, $p < 0.05$, Table 2b). The same result was obtained if wild broods of 7 from 1986 were excluded, and analysis of variance performed on the remaining groups. Growth rates for females in broods of 7, both captive and wild, were significantly slower than for captive broods of

2 and 5. Growth rates of females in these enlarged broods also tended to be slower than rates for wild broods of 2 and 5, although not significantly so.

For the two-level nested ANOVA, wild broods of 2 from 1986 and 1987 in which no pre-fledging mortality occurred were pooled since neither weight nor growth rate differed significantly between years for either sex (t-test, $p > 0.05$ in all 4 comparisons). Only nests from 1987 were analyzed for wild broods of 5 and 7, since for these 2 brood sizes all nests had at least one chick die prior to fledging in 1986. Significant differences existed among brood sizes for weight but not growth rate for both sexes. Differences among broods comprising an experimental group were significant for weight and growth rate of females, but not males (Table 3). Significant differences among brood sizes were attributable primarily to the lighter young fledging from wild broods of 7 (Table 4). Therefore, enlarging brood size appeared to influence fledging weight for wild kestrels. Furthermore, fledging weight and growth rates were influenced by membership in a particular brood, but only for females.

Weight parameters of young in broods of 7 were not influenced by parentage. For enlarged captive and wild broods from 1987, average fledging weights and growth rates were not significantly different between natural and foster young for either sex (t-test, $p > 0.05$). Comparisons could not be tested for wild broods from 1986 due to small sample sizes resulting from high pre-fledging mortality.

Growth rate constants were not correlated with asymptotic weight (for males, $r = -0.13$, 103 df and for females, $r = -0.12$, 96 df, $p >$

0.05), as K is only related to time to complete a given growth segment, independent of the absolute magnitude of that growth.

Tarsal and antebrachial length- Morphometric measurements for captive bred young from 1986 have been excluded from the following analyses, as they were consistently higher than all other groups. Pooled tarsal or antebrachial length for all captive young from 1986 was compared to pooled data from all other broods. In both comparisons captive young from 1986 had significantly longer measurements (t-test, $p < 0.001$). This discrepancy may have resulted from experimental artifact, since these were the only young measured by an assistant.

Variances between groups were homogeneous for both tarsal and antebrachial length (F test for equality of variances, $p > 0.05$). Based on all surviving young, significant differences were found among groups for both bone lengths (Table 5). Young from wild broods of 7 in 1987 exhibited a tendency toward shorter bones at fledging, particularly with respect to the antebrachium. This appeared primarily due to young fledging from broods of 7 where pre-fledging mortality had occurred. Nested ANOVAs based only on broods without pre-fledging mortality indicated that differences between groups were insignificant while differences among broods comprising a group were significant (Table 6). Thus, membership within a particular brood appeared, in general, to be the most important factor determining bone length at fledging.

Ninth primary length- Unlike skeletal features, the ninth primary had not reached an asymptotic length prior to fledging. Balgooyen

(1976) found a similar trend for the fourth remex. Furthermore, since age at the time of the last measurement varied by 2-3 days among young, it was not possible to ascertain primary length at fledging for all individuals. However, ninth primary length at day 22 (4-5 days pre-fledging) was known for a large number of young, and can give some indication of trends with respect to brood size. Data were pooled for sexes and between years for captive and wild broods as no significant differences occurred (t-test, $p > 0.05$, all comparisons). Young from wild broods of 7 had shorter ninth primaries at day 22 than young from wild broods of 2 and 5 (Table 7). There were no significant differences in feather length between young from captive and wild broods of equivalent size (t-test, $p > 0.05$ in all 3 cases).

DISCUSSION

Fledging success- The average number of young fledging from experimentally enlarged broods was slightly greater than from normal sized broods for captive kestrels, but only in 1 of 2 seasons for the wild population. However, these differences in productivity between broods of 5 and 7 were not significant. Some breeding pairs demonstrated that kestrels are capable of raising all members of an enlarged brood to fledging age. In the wild however, birds in broods where all 7 young survived were significantly lighter at fledging than other young, and the quality of these chicks may have been poorer.

Productivity of wild nests was highly variable between years (Appendix). In 1986, broods of 5 suffered heavy pre-fledging mortality, and productivity was no greater than that of a much smaller sized brood (2 young). In contrast, in 1987 all 7 breeding pairs raising a normal sized brood had 100% fledging success. The differences in fledging success between years mirrored differences in prey abundance (microtine rodents), which increased tenfold in 1987 as compared with 1986 (Chapter 2). Prey abundance in 1986 was possibly below average, preventing parents from finding adequate food to keep all young in a normal sized brood well fed, which resulted in the poor fledging success. Although long-term records of prey density are not known for this study area, the estimated prey abundance in 1987 was much higher than values reported in a previous study on the same population (Bowman and Bird 1986). This suggests that prey abundance that year was at or above average levels. Due to this high prey density, not only were young in normal sized broods well fed, but in several enlarged broods all young were kept adequately nourished. Korpimaki (1987) found similar results for Tengmalm's owls. Fledging success was positively correlated with Microtus vole abundance, and at least in peak vole years, birds could rear larger broods than their original clutch size.

Nest records for this population indicate that between 1983 and 1985, 6 of 9 nests with an initial brood size of 5 fledged 5 young, while the others fledged 4 (unpubl. data). Nests fledging only 4 young may have been located in territories with lower food abundance. Although not recorded, the dead chicks in these 3 nests may have been the last chick hatched. Death of this nestling could be due to facultative brood reduction when food resources are below average (Mock 1984). At 6 other nests, 5-egg clutches were laid, but the initial brood size was smaller due to the presence of infertile eggs. However, in these nests, all young which hatched survived until fledging.

The modal clutch size of the wild population was 5 eggs, and mean clutch size varied little between years. Nest records indicated that fledging success from broods of 5 was generally high. In 1986, when fledging success was poor, prey abundance may have been below average. These factors suggest that kestrels lay a 5-egg clutch in the expectation that prey abundance is high enough to support 5 young. This implies that brood size corresponds with the largest number of young which parents can feed (Lack 1954, 1968).

In the 2 enlarged wild broods from which all 7 young fledged in 1987, chicks weighed significantly less at fledging than young from normal sized broods. Similar patterns of higher productivity but decreased fledging weight have been reported for brood manipulation experiments with seabirds (Jarvis 1974, Lloyd 1977) and passerines (Crossner 1977, Bryant and Westerterp 1983). Korpimaki (1987) reported a similar trend in manipulated Tengmalm's owl broods, although differences in fledging weights were insignificant. Sex-ratios in the 2 wild broods from which 7 kestrels fledged were skewed in favor of males, i.e. both contained 5 males and 2 females. Competition among siblings for food may be dominated by the heavier female nestlings as Cavé (1968) suggested for Eurasian kestrels (F. tinnunculus). The prevalence of male chicks in these enlarged broods may have reduced size mediated competition during feeding bouts, such that food was more evenly distributed among all nestlings.

Furthermore, this chance predominance of male nestlings probably meant that the total energy demand of the brood was less than if the sex ratio was nearer 50:50, which may have enabled parents to keep all young at least adequately fed.

Time of breeding may have also influenced fledging success in these enlarged broods in 1987. All 7 young fledged from the earliest brood (hatch date 15 May). Two later enlarged broods (hatch date 1 and 5 June) fledged 7 and 5 young, respectively. Fledging weights of males were significantly higher in the early brood of 7 compared to the latter. Only 3 young fledged from the latest brood (hatch date 15 June).

Kestrels undergo a post-fledging weight recession (Balgooyen 1976) during which weight can drop by 10-20 g. Some of this weight loss may be due to changes in body H_2O content, such as water loss from feathers (Ricklefs 1968a), but this is unlikely to account for the entire weight change. Parents provide food in decreasing amounts to young for about 2 weeks after fledging (Lett and Bird 1987) during which time fledglings acquire hunting skills. Therefore, weight loss is most likely due to utilization of accumulated fat stores until young become adept at feeding themselves. Average adult weight is about 105 g for males and 120 g for females (Palmer 1988). Most young in this study fledged above adult weight and probably dropped to that weight after fledging. Young from wild broods of 7 in 1987 fledged at or below average adult weight. Hence, typical patterns of post-fledging weight change in these young may have resulted in mortality from emaciation. Although post-fledging mortality was not known, other studies have indicated that survival immediately following fledging is strongly correlated with fledging weight (Perrins 1965, Jarvis 1974, Loman 1977, Murphy 1978). Since juvenile kestrels form post-fledging feeding flocks (Lett and Bird 1987), small body size may also produce decreased post-fledging survival resulting from increased behavioural dominance by larger cohorts (Garnett 1981).

Six of 9 enlarged captive broods fledged 6 or more young. Of the other 3 nests, 2 fledged 4 young and one fledged 5. Differences in fledging success among these broods may be due to several factors. Haydock and Ligon (1986) found that manipulating broods of Chihuahuan ravens (Corvus cryptoleucus) to eliminate age and weight differences increased fledging success in comparison with less synchronous broods. Manipulations in my study attempted to minimize age differences, and in most cases ages varied by no more than one day. However, 2 of the 3 captive broods fledging 5 young or less had age ranges of 1-2 days. Weight increases rapidly in the first few days post-hatch and weight hierarchies resulting from age differences were not compensated for later in the nestling period. Therefore, although food was available ad libitum, younger nestlings were possibly outcompeted by older, larger siblings whenever parents fed, leading to death from starvation.

Slagsvold (1982) suggested that increased mortality associated with brood enlargement may be a result of nestbox crowding. This appears unlikely in my study, as nestboxes had identical dimensions, and captive broods showed no adverse effects of crowding on fledging success.

An increased number of young may produce other problems that lead to higher mortality. Nestboxes containing enlarged broods tended to be less sanitary due to the greater accumulation of fecal material on the walls and partially consumed prey carcasses in the bedding. This may increase the risk of young contracting disease or nest parasites as compared with young in small and normal sized broods, whose nestboxes tended to be cleaner.

In general, captive breeding kestrels provided with ad libitum food were capable of successfully rearing an enlarged brood. These results are comparable with field experiments where supplemental feeding done in conjunction with brood enlargement increased productivity (Crossner 1977). This supports the idea that food availability is the factor which regulates brood size.

Weight and growth rates- Asymptotic weight was relatively constant among groups. Only young from enlarged wild broods in 1987 showed a consistent trend toward decreased fledging weight, perhaps resulting from decreased per capita food consumption. Problems of thermoregulation caused by overheating in the nestbox and tissue dehydration may have magnified weight differences in these enlarged broods (Crossner 1977). For females, variation in fledging weights within brood sizes was as important as variation among brood sizes (Table 3). This was also true for growth rates of females. Similar patterns were not observed for males. This suggests that the larger, female young may have been more susceptible than males to changes in food availability. Differences in food availability among nests were more pronounced for broods in the wild than in captivity. Variations in prey abundance or parental hunting ability could account for differences in the amount of food available for wild young.

Growth rates of young from different groups, based on all surviving birds, were generally similar. Considering only those broods without pre-fledging mortality, growth rates among groups were not significantly different (Table 3). Ricklefs (1968b) noted that variations in food availability will influence asymptotic weights, but not rates of growth. Young from wild broods of 7 in 1987 illustrate this point. These young had lower asymptotic weights, but displayed no change in the rate at which those weights were reached. The lower fledging weights likely result from allocation of a greater proportion of the available energy to maintenance and tissue maturation at the expense of growth. Rates of development are not seriously affected unless nutritional deficiencies lead to starvation (Ricklefs 1968b). The depressed growth rates observed for the few young fledging from wild broods of 7 in 1986 may indicate that these birds were encountering nutritional deficiency. Chicks were able to attain normal fledging weights, but only after the mortality of siblings had lessened competition for food. The t_{10-90} period (time required to grow from 10 to 90% of asymptotic weight, Ricklefs 1967) for these young was 21 days against a mean of 13.5-14.5 days for other groups, illustrating that they took longer to reach fledging weights. Lenton (1984) found that increasing brood size from 6 to 7 at one barn owl (Tyto alba) nest resulted in starvation of some nestlings, and a t_{10-90} time of 42.7 days for surviving young compared with a population mean of 28 days.

Young raised in captivity were not faced with food limitation, irrespective of brood size. Growth rates for these young were therefore most likely limited by physiological constraints, specifically the rate at which food can be converted into metabolizable energy (Ricklefs 1969). Females from captive broods of 7 appear to contradict this hypothesis, as they exhibited significantly slower growth rates than birds in smaller broods. The reason for this is unclear, but is not likely a result of food limitation, as males from these broods did not show a similar trend.

In broods without pre-fledging mortality, growth rates of wild birds were slightly, but not significantly lower than rates for captive birds. Assuming captive raised young were limited by physiological constraints, this suggests that these wild birds were growing near their physiological maximum. Similar growth rates for captive and wild chicks have been reported in other studies on raptors (Lenton 1984, Collopy 1986). Martin (1987) suggested that altricial young rarely grow at their physiological maximum, but instead at a rate set by parental food delivery rates. The slightly slower growth rates of wild young relative to captive birds may be a function of declining growth rates as nestling age increased due to progressively greater competition for available food.

<u>Tarsal and antebrachial length</u>- In broods without pre-fledging mortality, mean bone lengths were not significantly different among brood sizes. Other studies on raptors also found no changes in bone length due to natural or experimental variations in brood size or fluctuating environmental conditions (Moss 1979, Korpimaki 1987,

Wilson et al. 1987). For both tarsal and antebrachial length, the particular brood in which young were reared contributed significantly to the total variance, suggesting that in general, appendage length may be more strongly determined by genetic factors than environmental fluctuations. Smith and Dhondt (1980) found that tarsal length of young in manipulated song sparrow (Melospiza melodia) broods was strongly correlated with tarsal length of their natural parents but not of their foster parents. While they caution that these results cannot be uncritically generalized to other species, they do point to skeletal features being largely influenced by hereditary factors.

Ninth primary length- Birds in experimentally enlarged wild broods had significantly shorter ninth primaries at 22 days of age than young in broods of 2 and 5. Although exact age at fledging was not determined, it is possible that young in broods of 7 may have fledged slightly older than other young. An inverse relationship between primary length and duration of the nestling period has been observed in manipulated tree swallow (Tachycineta bicolor) broods (DeSteven 1980). Development of primary feathers appears to be more easily influenced by environmental factors than tarsal or antebrachial development. Since primaries grow late in development, they may be more adversely affected by malnutrition in older nestlings (Price 1985).

Results from this study indicate that in this region 5 young is the largest brood size for which kestrels can, on average, provide food. This appears to support Lack's (1954, 1968) hypothesis regarding the evolution of clutch size. Reproductive success of parents with normal sized broods differed between years in relation to fluctuations in prey abundance. In 1986, parents could not meet the food demands of even broods of 5 and pre-fledging mortality was high. In 1987, growth rates and fledging weights of young in broods of 5 were comparable to those of young in experimentally reduced wild broods and captive broods fed from _ad libitum_ food. This suggests that for young in normal sized, wild broods in 1987 the probability of post-fledging survival was maximized. Wild kestrels were occasionally capable of rearing all chicks in larger than normal broods to fledging. Although young in these nests grew at rates similar to young in normal sized broods, they weighed significantly less at fledging. The poorer quality of these birds may have led to higher post-fledging mortality.

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TABLE 1. Average number of young fledging from manipulated American kestrel broods.

	BROOD SIZE	YEAR	N	$\bar{x} \pm 1$ SD
WILD NESTS*	2	1986	7	1.43 ± 0.98
		1987	5	1.80 ± 0.45
	5**	1986	5	1.80 ± 1.30
		1987	7	5.00 ± 0
	7*	1986	6	1.17 ± 2.04
		1987	4	5.50 ± 1.91
CAPTIVE NESTS	2	86/87	11	2.00 ± 0
	5	86/87	8	4.63 ± 0.74
	7	86/87	9	6.00 ± 1.32

* Mann-Whitney U test for differences between years, * $p < 0.05$; ** $p < 0.01$.

TABLE 2. Fledging weights and growth rates of all surviving nestlings in manipulated American kestrel broods.

a) <u>MALES</u>

BROOD SIZE	EXPT'L GROUP	N	WEIGHT (g)*	GROWTH RATE (K)*
2	Captive	10	132.9 ± 9.9^a	0.328 ± 0.047^a
	Wild 86	5	136.2 ± 12.9^a	0.308 ± 0.054^a
	Wild 87	5	136.8 ± 5.4^a	0.267 ± 0.024^a
5	Captive	11	135.6 ± 8.0^a	0.326 ± 0.054^a
	Wild 86	4	128.3 ± 12.2^a	0.253 ± 0.030^a
	Wild 87	21	132.1 ± 11.4^a	0.292 ± 0.058^a
7	Captive	31	134.1 ± 10.4^a	0.306 ± 0.079^a
	Wild 86	3	131.0 ± 6.9^a	0.207 ± 0.015^a
	Wild 87	15	110.3 ± 10.7^b	0.285 ± 0.063^a

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* For each variable, values within the column sharing a common superscript are not significantly different (t-test, $p > 0.05$).

TABLE 2 (cont.)

b) <u>FEMALES</u>

BROOD SIZE	EXPT'L GROUP	N	WEIGHT (g)*	GROWTH RATE (K)*
2	Captive	12	147.8 ± 7.5^{ab}	0.310 ± 0.035^{ab}
	Wild 86	5	156.8 ± 14.0^{a}	0.284 ± 0.019^{abc}
	Wild 87	4	148.6 ± 22.4^{ab}	0.314 ± 0.022^{ab}
5	Captive	25	146.0 ± 12.8^{ab}	0.327 ± 0.061^{a}
	Wild 86	6	116.4 ± 14.5^{c}	0.301 ± 0.076^{abc}
	Wild 87	14	146.9 ± 14.0^{ab}	0.281 ± 0.045^{bc}
7	Captive	21	144.1 ± 11.3^{b}	0.249 ± 0.057^{cd}
	Wild 86	4	145.0 ± 12.2^{ab}	0.205 ± 0.005^{d}
	Wild 87	7	119.2 ± 12.8^{c}	0.259 ± 0.037^{c}

* For each variable, values within the column sharing a common superscript are not significantly different (t-test, $p > 0.05$).

TABLE 3. Two-level nested analysis of variance for fledging weight and growth rate in manipulated American kestrel broods. Six experimental groups were analyzed; broods of size 2, 5, and 7 for both captive and wild populations.

a) MALES

	WEIGHT			GROWTH RATE (K)		
SOURCE	df	MS	F	df	MS	F
Experimental group	5	1409.6	3.48*	5	0.0053	1.35
Brood within expt'l group	28	404.7	0.43	28	0.0040	1.06
Within broods	47	945.7		47	0.0037	

b) FEMALES

	WEIGHT			GROWTH RATE (K)		
SOURCE	df	MS	F	df	MS	F
Experimental group	5	857.8	3.12*	5	0.0098	2.38
Brood within expt'l group	28	275.1	3.33**	28	0.0041	3.13**
Within broods	38	82.7		38	0.0013	

* $p < 0.05$; ** $p < 0.005$.

TABLE 4. Fledging weights and growth rates of American kestrels in manipulated broods, based only on nests not experiencing pre-fledging mortality.

a) MALE

STATUS	BROOD SIZE	N	WEIGHT (g)*	GROWTH RATE (K)*
Captive	2	10	132.9 ± 9.8^{ab}	0.328 ± 0.047^{a}
	5	9	132.8 ± 5.3^{ab}	0.335 ± 0.051^{a}
	7	21	130.5 ± 6.4^{b}	0.326 ± 0.076^{a}
Wild	2	10	136.5 ± 9.3^{a}	0.286 ± 0.046^{a}
	5	21	132.1 ± 11.3^{ab}	0.292 ± 0.058^{a}
	7	10	109.5 ± 12.2^{c}	0.305 ± 0.068^{a}

b) FEMALE

STATUS	BROOD SIZE	N	WEIGHT (g)*	GROWTH RATE (K)*
Captive	2	12	147.8 ± 7.4^{a}	0.310 ± 0.035^{a}
	5	20	144.3 ± 12.8^{a}	0.325 ± 0.065^{a}
	7	14	144.4 ± 12.2^{a}	0.254 ± 0.056^{a}
Wild	2	8	156.1 ± 16.1^{a}	0.292 ± 0.020^{a}
	5	14	146.9 ± 14.0^{a}	0.281 ± 0.045^{a}
	7	4	116.9 ± 16.3^{b}	0.278 ± 0.028^{a}

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* For each variable, values within the column sharing a common superscript are not significantly different (t-test, $p > 0.05$).

TABLE 5. Bone measurements of all surviving nestlings in manipulated American kestrel broods. Sexes have been pooled for analysis.

BROOD SIZE	EXPT'L GROUP	N	TARSAL LENGTH[*]	ANTEBRACHIAL LENGTH[*]
2	Captive	10	39.8 ± 0.8^{ab}	50.7 ± 1.8^{ab}
	Wild 86	10	40.1 ± 1.8^{ab}	51.2 ± 1.8^{a}
	Wild 87	9	39.8 ± 1.6^{abc}	49.6 ± 1.4^{bc}
5	Captive	10	40.2 ± 1.5^{a}	51.3 ± 1.1^{a}
	Wild 86	10	38.6 ± 1.3^{c}	50.8 ± 2.3^{ab}
	Wild 87	35	40.5 ± 1.6^{a}	50.1 ± 2.4^{ab}
7	Captive	14	40.0 ± 1.2^{a}	50.4 ± 1.3^{ab}
	Wild 86	7	39.5 ± 1.3^{abc}	51.2 ± 1.7^{ab}
	Wild 87	22	39.0 ± 1.6^{bc}	48.6 ± 2.3^{c}

[*] For each variable, values within the column sharing a common superscript are not significantly different (t-test, $p > 0.05$).

TABLE 6. Two-level nested analysis of variance for tarsal and antebrachial length in manipulated American kestrel broods. Six experimental groups were analyzed; broods of size 2, 5, and 7 for both captive and wild populations. Sexes have been pooled for analysis.

	TARSAL LENGTH			ANTEBRACHIAL LENGTH		
SOURCE	df	MS	F	df	MS	F
Experimental group	5	2.35	0.63	5	4.56	0.59
Brood within expt'l group	21	3.73	2.00*	21	7.74	3.20**
Within broods	74	1.87		74	2.41	

* $p < 0.05$; ** $p < 0.005$.

TABLE 7. Length of the ninth primary feather at day 22 of the nestling stage for American kestrels in manipulated broods. Data have been pooled between years and sexes for all groups. Values in parentheses refer to the number of young measured.

	NINTH PRIMARY LENGTH (mm)[*]	
BROOD SIZE	Wild Broods	Captive Broods
2	66.5 ± 4.3^{a} (14)	64.1 ± 4.0^{a} (7)
5	63.7 ± 5.8^{a} (28)	64.3 ± 4.9^{a} (10)
7	58.5 ± 5.2^{b} (21)	60.5 ± 9.2^{a} (12)

[*] Values within a column sharing a common superscript are not significantly different (t-test, $p > 0.05$).

CONNECTING STATEMENT

Chapter 1 described the growth and fledging success of nestling American Kestrels in captivity and in the wild in response to an experimental manipulation of brood size. These parameters are, in large part, influenced by the responses of parents to changes to the original brood size.

In Chapter 2, behavioural responses of wild breeding pairs to manipulation of brood size will be discussed and related to estimated prey abundance on the breeding territory.

CHAPTER 2

BEHAVIORAL RESPONSES OF AMERICAN KESTRELS TO MANIPULATED BROOD SIZES

ABSTRACT

Behavioral responses of American Kestrel (Falco sparverius) parents to manipulated brood sizes were studied in southwestern Quebec during 1986 and 1987. Broods of 2, 5, and 7 young were examined. Average territory size was significantly smaller in 1987 than 1986, but was not influenced by brood size in either year. Territory size was, however, inversely correlated with small mammal abundance which differed significantly between years. Time activity budgets revealed that parents of all 3 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 brood sizes. Despite less time spent hunting, rates of prey capture and food delivery to the nest were significantly higher in 1987. Adaptive constraints on parental foraging behavior is suggested as the most important factor limiting brood size in American Kestrels.

INTRODUCTION

Lack (1954, 1968) theorized that brood size in nidicolous birds is determined by the ability of parents to provide sufficient food to keep all young in the brood well nourished. Parental ability may be limited either by the abundance of the food supply or by adaptive constraints on their feeding behavior. According to Lack's 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 until 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 as low recovery rates of banded individuals necessitate very 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).

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. This procedure does not permit one to ascertain subsequent adult survival, but can indicate whether parents respond to changes in brood size by modifying foraging expenditure, or whether parents are already at the limit of their reproductive capabilities as Lack (1954, 1968) suggested. I report here on the influence of experimental manipulation of brood size on parental behavior and feeding frequency in the American Kestrel (Falco sparverius). This was done in conjunction with a study investigating the effect of alteration of brood size on growth and fledging success of nestling kestrels (Chapter 1).

METHODS

This study was performed in 1986 and 1987 in southwestern Quebec. The study area has been described elsewhere, as has the experimental protocol used for brood size manipulations (Chapter 1). Considering broods of 5 to produce, on average, the greatest number of surviving young, I manipulated broods to create small and large broods of 2 and 7 young, respectively.

Parental behavior was recorded during observation periods of 2 h duration. Observations were made from partially concealed positions about 50-100 m from the nestboxes, and were performed throughout the nestling period. Observation sessions were early morning (0700-1100) and late afternoon (1500-1700). To eliminate bias due to pre-fledging mortality, observations were only done at nests where all young were still 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 1 of 5 categories: hunting, perched, maintenance, brooding or feeding 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. Brooding or feeding of the young could not be observed directly, but was inferred from time parents spent in the 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, rates of prey capture and the number of food deliveries to the nest were recorded. Prey capture rates were determined either directly by viewing kestrels diving to the ground 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 near active nests. Trapping was done at locations where kestrels were observed hunting, and in vegetatively similar habitat. At each site, 36 Victor snap traps, baited with peanut butter and rolled oats, were laid out 5 m apart in a 6x6 grid arrangement. Traps were checked each morning for 10 consecutive days. A relative index of abundance was calculated according to the formula:

$$\begin{array}{l}\text{Number of captures}\\ \text{per 100 trap nights}\end{array} = \frac{(\text{Number of captures})*(100)}{(\text{Trap nights})-(\text{Sprung} + \text{missing traps})}$$

where 1 trap set for 10 nights = 10 trap nights (U.S.D.I. 1979).

On at least 4 occasions during the nestling period, sweep-netting 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.

Breeding territory size was determined by 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, home range was considered as the maximum polygon area created by connecting the outermost locations to form a convex polygon (Odum and Kuenzler 1955). Area of the home range 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 $\pm$ 1 SD.

RESULTS

Kestrels maintained smaller breeding territories in 1987 than in 1986. Parents of all 3 brood sizes displayed this trend, with differences between years for average territory area being significant for parents raising broods of 2 or 5 young (Table 1). However, within each year there was no significant difference in territory size corresponding with variations in brood size (Kruskal-Wallis test, $p > 0.05$ for both years).

Average small mammal abundance, as estimated by snap-trapping, was 3.84 $\pm$ 4.03 mammals/100 trap nights in 1986 ($n = 10$ trap sites), and 38.23 $\pm$ 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 caught in total), and 97.1% in 1987 (725 mammals caught). Shrews (*Sorex cinereus*, *Blarina brevicauda*) composed 22.6% of the total in 1986 and 1.9% in 1987. Deer mice (*Peromyscus* *maniculatus*) formed the remainder of the total percentage in both years. Territory size exhibited a significant negative correlation with estimated prey abundance at that locality (Spearman's $r_s = -0.770$, $n = 17$, $p < 0.005$, 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 2 neighboring nests with different brood sizes. Qualitatively, vegetative structure in these breeding territories and at the trap site appeared similar, 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 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.

A total of 77.67 h of observations on parental behavior were made in 1986, and 60.60 h in 1987. Time activity budgets revealed that parents of all brood sizes devoted less time to hunting in 1987 than in 1986 (Fig. 2). Differences were significant for both parents with broods of 2, and for females with broods of 7 (Mann-Whitney U test; $p < 0.05$). For males rearing broods of 7, 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, $p > 0.05$). Although males of all brood sizes spent more time hunting than females, the differences were only significant for broods of 2 and 5 in 1986 and broods of 7 in 1987 (Mann-Whitney U test, $p < 0.05$ in all 3 cases). Kestrels compensated for decreased hunting time in 1987 by allotting more time to resting or maintenance activities (Fig. 3). Parents of all 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 2 and 7 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 5 in 1986 and broods of 7 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 (Fig. 4). Early in the nestling stage females probably devoted most of their time to brooding young until the young 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 virtually no time in direct care of the young regardless of brood size.

Interspecific behavior against other birds, either aggressive or defensive, accounted for less than 0.5% of the total activity budget and has 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 2). Parents of all brood sizes had greater hunting success in 1987 as compared with 1986, with differences being significant for parents raising broods of 2 and 7. Within each year however, there was no significant difference in hunting success among brood sizes (Kruskal-Wallis test, $p > 0.05$, for both years).

The proportion of invertebrates to vertebrates in total prey captures was not known, but sweep netting 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) likely took place at this time. Therefore, insects probably did not constitute a major part of the diet of parents during the nestling period.

Trends in the rate of vertebrate prey deliveries to young paralleled those observed for prey capture rates (Table 2). 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 3 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 7 in 1987 (Table 2). Within each year, the rate of food delivery was not related to brood size (Kruskal-Wallis test, $p > 0.05$, for both years).

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) on the same population which reported a similar inverse relationship between prey abundance and territory size. Microtine rodent abundance in the earlier study was similar to my estimates for 1986, and territory sizes during these 2 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 in response to changes in energetic demands associated with modifications of 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. Also, prey density in the territory may have been sufficiently high that parents with enlarged broods were able to increase capture rates without having to expend more energy by hunting over a wider area.

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 5 and 7 in 1986 (Chapter 1), indicating that parents were unable to adequately nourish normal or enlarged sized broods. This mortality probably further lowered feeding rates at these nests by lessening the total energetic demand.

Since nestling mortality was low in 1987 (Chapter 1), dividing average feeding frequencies by brood size gives an approximation of feedings per nestling (Fig. 5). For broods of 7, several values from nests where mortality had decreased brood size below 7 were excluded. The rate of feeding per nestling declined with increasing brood size in a concave manner similar to that predicted by a model of optimal feeding frequency (Nur 1984b). Young in smaller than average sized broods were fed at higher rates than young in average or above average sized broods where rates were nearly equal. Despite this, fledging weights for young in broods of 2 and 5 were similar while young in broods of 7 fledged significantly lighter (Chapter 1). Nur (1984b) suggested that mean prey size decreases as brood size increases due to the inclusion of a greater number of smaller prey items. If this was true in my study, then although feeding rates per individual remained constant, the mass of food delivered per trip might have been lower for broods of 7 young. Increased feeding frequency of young in small broods did not translate into increased weight at fledging as Nur (1984b) found for Blue Tits (<u>Parus caeruleus</u>). Kestrels in smaller than average broods may be expending more energy to maintain homeothermy than young in larger broods (Royama 1966, O'Connor 1975).

In relative terms, 1987 was a much higher density prey year than 1986. Thus, parents with broods of 2 and 5 spent less time hunting in 1987 than in 1986. The trend toward decreased hunting time might be expected since greater prey abundance and enhanced hunting success in 1987 meant that kestrels could capture sufficient food to meet nestling and adult requirements in a shorter span of time than in 1986. Parents rearing 7 young also spent less time hunting in 1987. Several pairs of kestrels were capable of raising all young in a brood of 7 to fledge in 1987, although these young fledged significantly lighter than young in broods of 5 (Chapter 1). 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 limits upon parental feeding behavior as stated by Hussell (1972) and Nur (1984b).

Hover-hunting never accounted for more than 20% of the total time spent hunting, a ratio corresponding with values reported in other studies (Balgooyen 1976, Rudolph 1982, Toland 1987). The proportion of time spent hover-hunting was larger in 1987 due to the relatively greater use of perch-hunting in 1986 than in 1987. This is in accord with a theoretical model which predicts switching to energetically less expensive hunting methods when prey abundance declines (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. Counteracting this, energetic consumption during hovering and forward flight is estimated to be about 7 times greater than while at rest (Rudolph 1982). 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 were presumably 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 my study, most territories were in undisturbed fields where vegetative 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 suggests that kestrels were at an energetic ceiling for this activity. Increasing time engaged in hover-hunting behavior may have incurred physiological costs to the parent, outweighing benefits expressed as increased prey capture rates and hence, increased offspring feeding rates (Nur 1984b). This would seem to contradict Rudolph's (1982) assertion that kestrels maximize energy acquisition above parental requirements instead of maximizing energetic efficiency.

For American Kestrels, 5 young, the normally occurring brood size appears to be the largest that parents can raise successfully without sacrificing offspring quality. More young may fledge from enlarged broods, but their poorer condition at fledging may increase post-fledging mortality. Food availability is a contributing factor regulating brood size, especially when prey abundance is low, e.g. 1986. Adaptive constraints on parental behavior appear to be more important. If parents raising 7 young in 1987 had increased hover-hunting behavior without varying the total time spent hunting, rates of prey capture may have improved, resulting in higher rates of prey delivery to the young and consequently, higher fledging weights. The lack of variation in hovering behavior suggests that kestrels were at an energetic maximum for this activity. Spending more time hover-hunting might have lowered the cost-benefit ratio for the parent. Habitat physiography is apparently a contributing factor. If territories were situated in short grass fields, rates of prey detection for the less effective but energetically cheaper perch-hunting strategy may have been sufficiently high to provide the additional food required to adequately feed an enlarged brood.

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TABLE 1: Size of breeding territories (in hectares) of American Kestrels in relation to brood sizes established by experimental manipulation.

	1986		1987	
BROOD SIZE	N	$\bar{x} \pm SD$	N	$\bar{x} \pm SD$
2	7	21.3 ± 4.0	5	11.3 ± 2.1 **
5	4	27.6 ± 7.6	6	12.4 ± 2.9 *
7	5	22.5 ± 5.0	4	16.3 ± 5.9
Pooled	16	23.2 ± 5.6	15	13.1 ± 4.0 **

* $p < 0.05$; ** $p < 0.01$, Mann-Whitney U test, for differences between years.

TABLE 2: Capture rates for vertebrate prey and delivery rates to the nest by American Kestrels raising various sized broods ($\bar{x}$ ± SD).

		YEAR	
	BROOD SIZE	1986	1987
PREY CAPTURE (prey items/hr)	2	0.51 ± 0.41	1.37 ± 0.95 *
	5	0.44 ± 0.73	0.88 ± 1.20
	7	0.26 ± 0.39	0.99 ± 0.80 **
	Pooled	0.41 ± 0.49	1.03 ± 0.96 **
PREY DELIVERY (prey items/hr)	2	0.33 ± 0.56	0.58 ± 0.47
	5	0.25 ± 0.38	0.45 ± 0.69
	7	0.18 ± 0.29	0.91 ± 0.77 **
	Pooled	0.26 ± 0.43	0.70 ± 0.70 **

* $p < 0.05$; ** $p < 0.01$, Mann-Whitney U test, for differences between years.

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

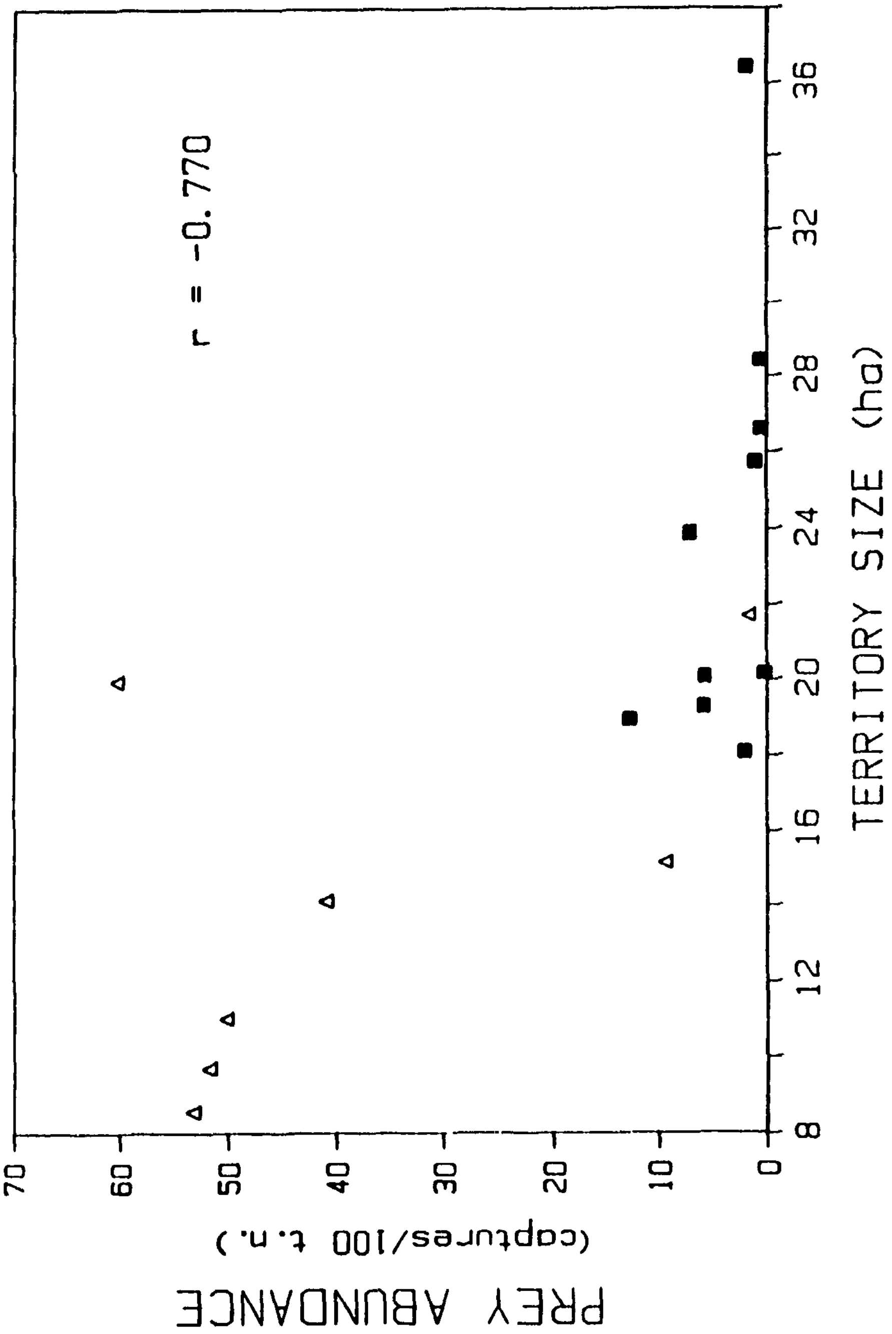

r = -0.770
PREY ABUNDANCE
(captures/100 t.n.)
0
10
20
30
40
50
60
70
TERRITORY SIZE (ha)
8
12
16
20
24
28
32
36

FIG. 2: Percent hunting time of American Kestrels raising various sized broods. Total time spent hunting is divided into perch-hunting and hover-hunting components. Numbers on the abscissa denote year (1986, 1987) and brood size (2,5,7). Values that are significantly different between years for each brood size are denoted on the graphs.

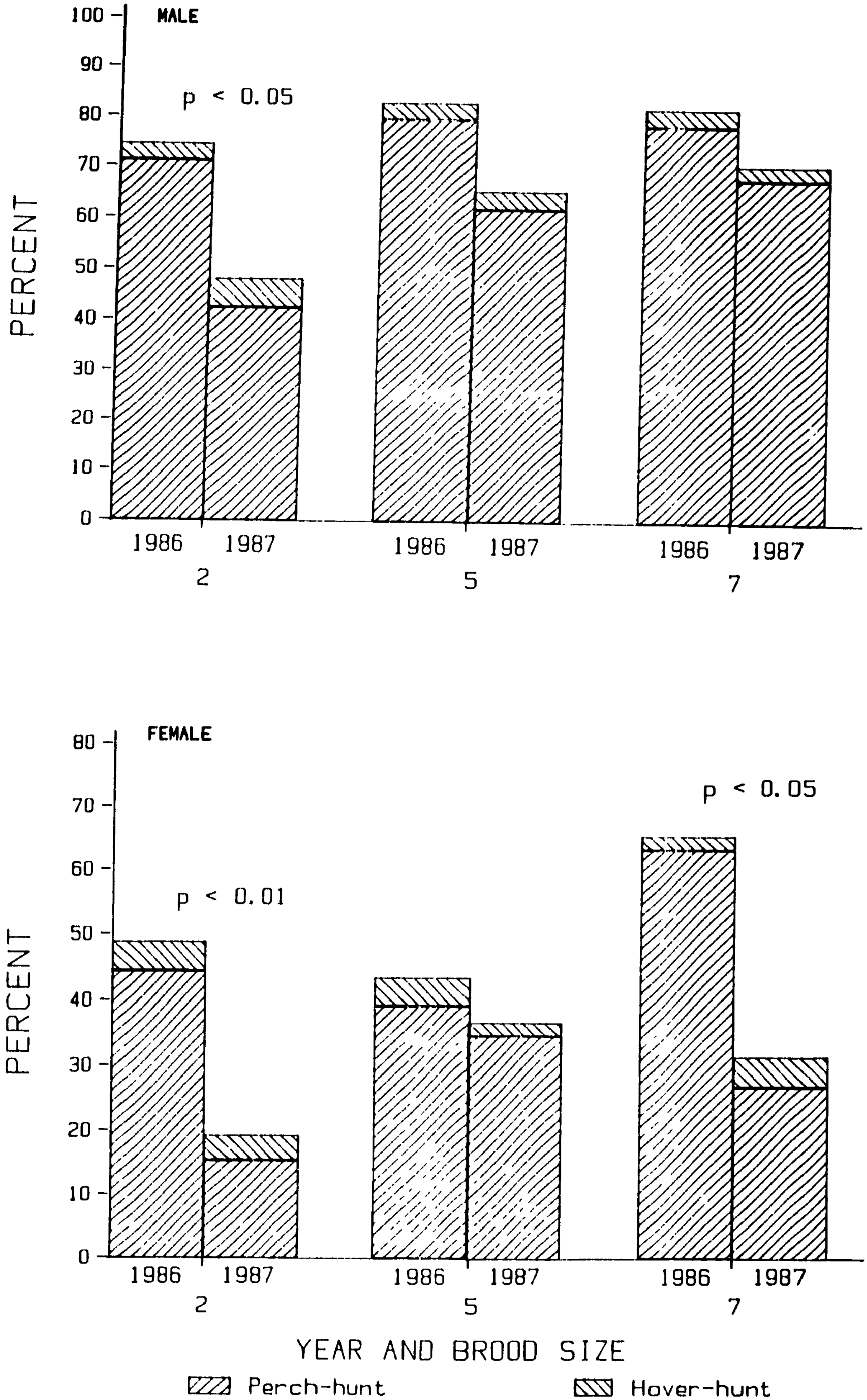

MALE
PERCENT
100
90
80
70
60
50
40
30
20
10
0
p < 0.05
1986
1987
2
1986
1987
5
1986
1987
7
FEMALE
PERCENT
80
70
60
50
40
30
20
10
0
p < 0.01
p < 0.05
1986
1987
2
1986
1987
5
1986
1987
7
YEAR AND BROOD SIZE
Perch-hunt
Hover-hunt

FIG. 3: Percent of total time devoted to resting or maintenance behavior for American Kestrels raising various sized broods. Numbers on the abscissa denote year (1986, 1987) and brood size (2,5,7).

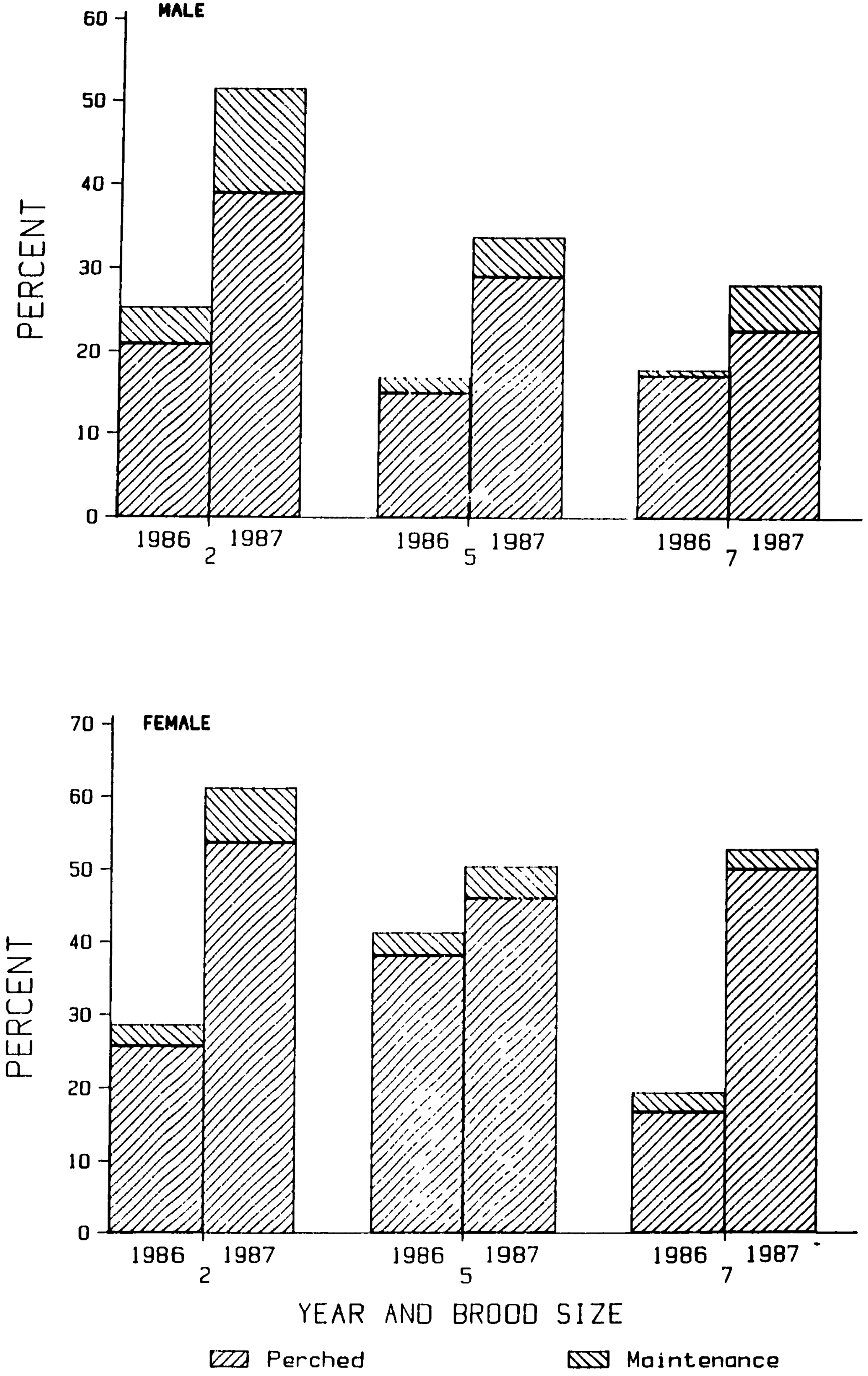

MALE
PERCENT
0
10
20
30
40
50
60
1986
1987
2
1986
1987
5
1986
1987
7
FEMALE
PERCENT
0
10
20
30
40
50
60
70
1986
1987
2
1986
1987
5
1986
1987
7
YEAR AND BROOD SIZE
▨ Perched
▧ Maintenance

FIG. 4: Percent of total time spent by American Kestrel parents brooding and feeding young in relation to brood size. Numbers on the abscissa denote year (1986, 1987) and brood size (2,5,7).

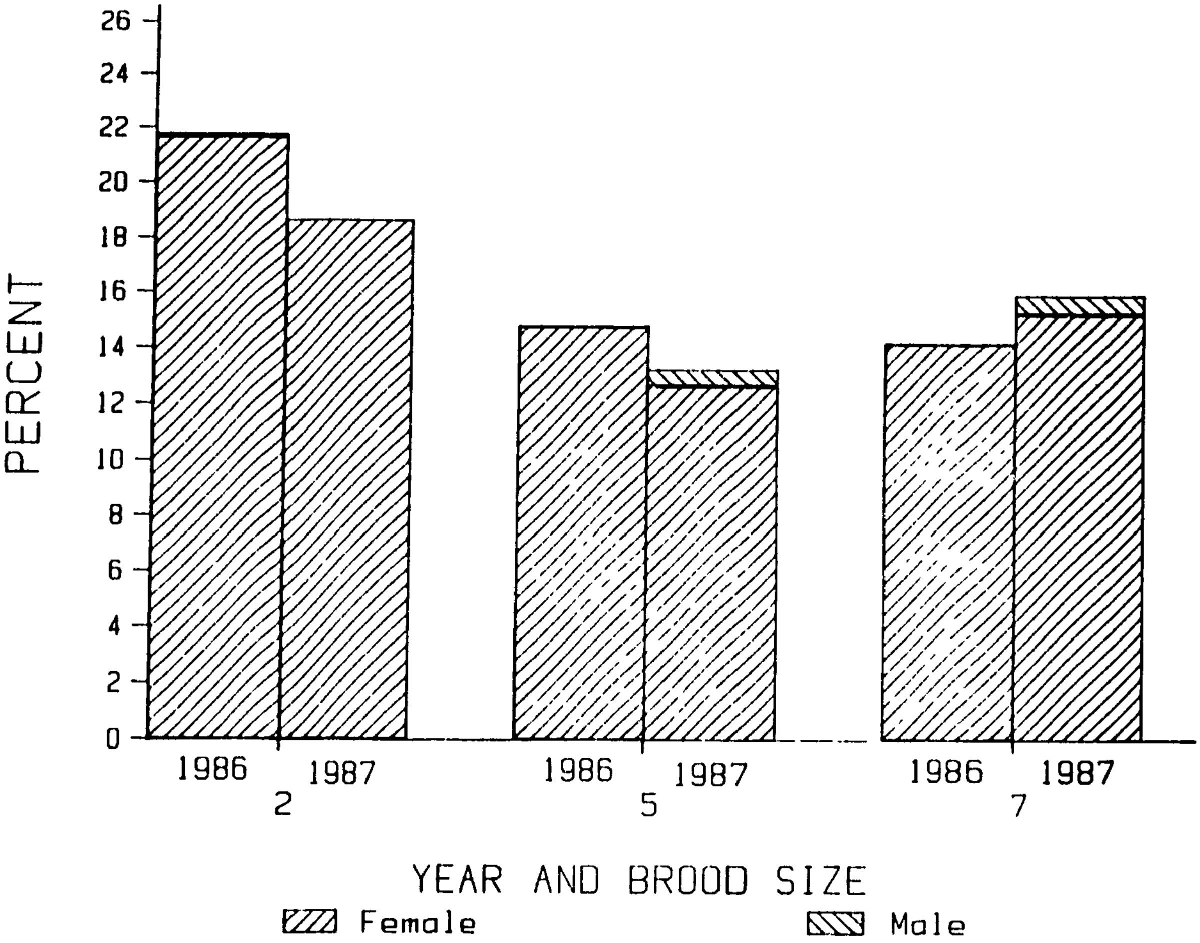
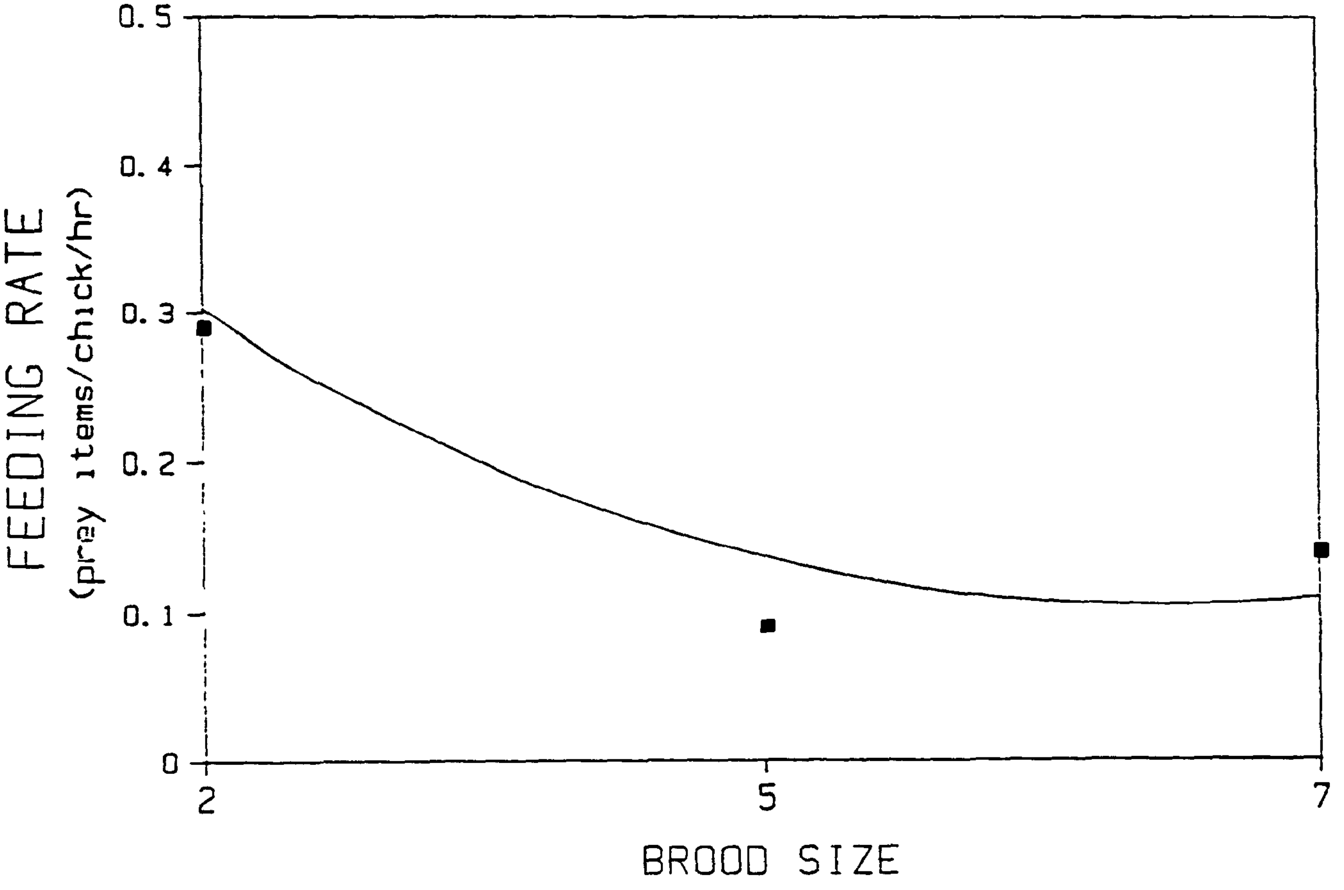

PERCENT
26
24
22
20
18
16
14
12
10
8
6
4
2
0
1986
1987
2
1986
1987
5
1986
1987
7
YEAR AND BROOD SIZE
Female
Male

FIG. 5: Average feeding rate of American Kestrel chicks in 1987 in relation to brood size.


0.5
0.4
0.3
0.2
0.1
0
FEEDING RATE
(prey items/chick/hr)
2
5
7
BROOD SIZE

GENERAL CONCLUSIONS

For the wild population of American Kestrels studied, enlarging brood size to 7 young did not produce a significant increase in the average number of birds fledging when compared with broods of 5, the largest naturally occurring brood size. In the 2 cases where parents were capable of rearing all 7 young to fledging, chicks weighed significantly less at fledging than birds in smaller sized broods. The fate of these birds after fledging was not known, but evidence from brood manipulation studies on other avian species suggests that survival after fledging is correlated with fledging weight. Fledging success in broods of 5 differed significantly between years. In 1986, pre-fledging mortality was high, while in 1987 no pre-fledging mortality occurred at any nest. These interannual differences paralleled shifts in prey (small mammal) abundance.

Excluding broods which were subject to pre-fledging mortality, young in wild broods of 5 grew at similar rates, and had similar weights and bone lengths at fledging as young in wild broods of 2 and captive reared broods of 5. This suggests that young in these wild broods of 5 were well-nourished and that the probability of survival post-fledging was high.

These results suggest that the observed average brood size of the population corresponds with the largest brood size for which kestrels can, on average, provide food.

In captivity, where food was available *ad libitum*, young in broods of 7 grew as well as young in smaller sized broods of 5. Comparable results might be expected for the wild population were brood size enlargement done in conjunction with the provision of supplemental food.

The ability of parents to feed young may be regulated by adaptive constraints on foraging expenditure. Parents decreased total hunting time as prey density increased. However, the proportion of time devoted to energetically expensive but more efficient hover-hunting remained constant despite changes in prey density or brood size. This behaviour may represent an adaptive ceiling on parental ability, such that even when prey density is high (e.g. 1987), the amount of time parents can spend hunting is constrained. This would limit the rate at which parents can provide food to the young. Thus, brood size appears to be regulated by both food abundance and behavioural constraints on parental foraging activity.

Fostering of captive bred young into wild nests has been suggested as a potential management technique to increase population sizes for endangered species of raptors. Results from my study indicate that caution should be taken before this approach is adopted. Parents may be incapable of maintaining all young in enlarged broods in good quality, even during years of high prey densities. If breeding birds will use artificial feeding stations, then fostering of captive young may be a valuable management technique if it is carried out simultaneously with a program of supplemental feeding.

APPENDIX: Chronology of nestling mortality in all American Kestrel broods used in this study.

a)Wild Broods- 1986

Nest	Original Brood Size	Manipulated Size	Number of Young Alive Until Day: 6	12	18	Fledging
DV-12	3	2	2	0	0	0
W-31	5	2	2	2	2	2
P-16	5	2	2	2	2	2
DV-9	5	2	2	2	2	2
W-14	5	2	2	2	2	2
DV-19	4	2	2	2	2	2
DV-4	5	2	2	2	0	0
W-28	5	5	5	5	4	3
W-25	5	5	5	4	3	1
W-26	5	5	5	5	2	2
P-13	5	5	5	5	4	3
W-9	4	5	4	0	0	0
DV-1	4	7	7	7	4	2
W-29	5	7	7	6	6	0
P-1	4	7	0	0	0	0
W-15	5	7	7	3	0	0
DV-23	5	7	6	6	5	5
DV-24	5	7	7	0	0	0

b)Wild Broods- 1987

Nest	Original Brood Size	Manipulated Size	Number of Young Alive Until Day: 6	12	18	Fledging
DV-12	3	2	1	1	1	1
DV-18	3	2	2	2	2	2
W-14	3	2	2	2	2	2
DV-2	4	2	2	2	2	2
P-17	5	2	2	2	2	2
DV-1	5	5	5	5	5	5
DV-22	5	5	5	5	5	5
DV-16	4	5	5	5	5	5
W-25	5	5	5	5	5	5
P-16	5	5	5	5	5	5
DV-24	5	5	5	5	5	5
W-15	4	5	5	5	5	5

b)Wild Broods- 1987 (cont.)

Nest	Original Brood Size	Manipulated Size	Number of Young Alive Until Day: 6	12	18	Fledging
DV-19	5	7	7	7	7	7
W-26	5	7	7	7	7	7
P-4	4	7	7	6	5	5
DV-23	6	7	7	7	5	3

c)Captive Broods

Pen	Original Brood Size	Manipulated Size	Number of Young Alive Until Day: 6	12	18	Fledging
C6	5	2	2	2	2	2
C8	4	2	2	2	2	2
C13	5	2	2	2	2	2
C12	4	2	2	2	2	2
C15	3	2	2	2	2	2
D26	3	2	2	2	2	2
C11	4	2	2	2	2	2
C9	2	2	2	2	2	2
C14	3	2	2	2	2	2
C18	3	2	2	2	2	2
C12	2	2	2	2	2	2
C10	5	5	5	5	5	5
D2	4	5	5	4	4	4
D8	5	5	5	5	5	5
E4	4	5	5	5	5	5
D12	5	5	3	3	3	3
E19	4	5	5	5	5	5
C5	5	5	5	5	5	5
C30	4	5	5	5	5	5
C1	5	7	6	6	6	6
C3	5	7	7	6	6	5
C7	4	7	7	7	7	7
C17	5	7	7	7	7	7
C28	4	7	7	7	7	7
D4	5	7	7	5	4	4
E6	4	7	6	5	5	4
C29	5	7	7	7	7	7
C16	5	7	7	7	7	7