

REPRODUCTIVE SUCCESS OF AMERICAN KESTRELS: THE ROLE OF PREY ABUNDANCE AND WEATHER¹

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Abstract. We investigated how natural variation in abundance and availability of the main prey of American Kestrels (*Falco sparverius*), small mammals, influenced provisioning rates by parents, and offspring size and survival. Provisioning behavior of kestrels was not constrained by the abundance of food in the environment; however, the availability of food, mediated through variation in weather, appeared to significantly influence parental provisioning behavior. Moreover, variation in weather had clear effects on reproductive success because nestlings exposed to inclement weather were smaller and lighter at fledging, and less likely to survive to fledging, compared to nestlings raised during good weather conditions. Prey abundance was not related to offspring size or survival. Our results suggest American Kestrels are limited by the availability, as opposed to abundance, of food on territories. It is likely that during our study, prey abundance was above some minimum threshold necessary to support successful reproduction, and so variation in weather affected reproduction more than variation in prey abundance.

Key words: American Kestrels, *Falco sparverius*, offspring size, offspring survival, prey abundance, provisioning, weather.

INTRODUCTION

Variation in food supply is thought to be an important determinant of reproductive success in birds, potentially affecting life-history traits such as the number and quality of young that parents are able to raise (Martin 1987, Boutin 1990). The assumption that reproduction of birds is food-limited can be traced to Lack (1947), who argued that clutch sizes of altricial birds were limited by the ability of parents to feed their offspring. Results from studies where brood size has been experimentally increased has supported the idea that food is limiting (Stearns 1992); however, brood enlargements do not address whether food limits reproduction of naturally-sized broods (Simons and Martin 1990). Similarly, experimental food manipulations often have been effective in altering reproductive variables only when natural food supplies were at extremes (Boutin 1990, Wernham and Bryant 1998). Taken together, these studies suggest that although food may limit reproduction of some birds, such effects may only occur in poor years.

Here, we determine the influence of natural variation in food supply on parental provisioning of American Kestrels (*Falco sparverius*), and its consequences for offspring. Using video cameras, we quantified the number and biomass of prey brought to nests by parents. Kestrels on our study area prey primarily on small mammals during the breeding season (Bortolotti et al. 1991), and we assessed abundance of mammals on a per territory basis. Martin (1995) predicted that, all else being equal, increases in food supply may increase condition and survival of young while reducing parental foraging time and reproductive costs. Food abundance is therefore expected to correlate positively with rates of parental provisioning, and consequently offspring size and survival. Similarly, provisioning rates, offspring size and survival are expected to be higher in good food years than in poor food years.

Although kestrels may adjust their reproductive strategies to the abundance of prey on territories (Bortolotti et al. 1991, Wiebe and Bortolotti 1992, 1994b, 1995), factors that affect prey availability may be equally or more important. In particular, variation in weather can significantly affect parental prey-provisioning rates in raptors (Simmons 1986) and other birds (Rodenhouse and Holmes 1992). Activity of rodents generally declines during inclement weather

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(Lehmann and Sommersberg 1980) and so prey may be less available to kestrels when weather conditions are poor. In addition to investigating effects of prey abundance on reproduction of kestrels, we also tested how availability of prey, mediated through weather, affected parents and offspring.

METHODS

We studied American Kestrels breeding in nest boxes in the boreal forest of northern Saskatchewan, Canada (55°N, 106°W) from 1993 to 1995. Approximately 370 nest boxes were placed in a variety of habitats, ranging from forested roadsides to open clearcuts, and 150–200 pairs bred in them annually. Kestrels arrived on our study area in mid to late-April, and egg-laying commenced in mid-May. Each nest box was visited every 3 to 5 days from mid-May to mid-June, or until egg laying had begun. We returned when laying was complete to ascertain clutch size. To avoid potentially confounding effects of clutch size in our analyses, we used only nests that had five eggs, the modal clutch size. The majority of these nests hatched five young, but in some cases partial hatching failure resulted in fewer than five young being present in a nest. At these nests we added foster young from nests not used in this study to maintain a brood size of five nestlings.

NATURAL VARIATION IN FOOD ABUNDANCE

We assessed abundance of food on each kestrel territory by censusing the main prey of kestrels, small mammals (Bortolotti et al. 1991). During the brood rearing period of each year (early July), trap lines consisting of 10 stations spaced 30 m apart and situated parallel to, and 10 m from, a road were set on all territories. At each station two snap traps were baited with peanut butter. Each line operated for 3 days, and traps were reset each morning. At stations where both traps had been sprung, we assumed that traps were available for only half the time and so a corrected number of available traps was used. Data were standardized to mean number of animals per 100 trap nights. Although kestrels prey on a variety of mammalian species, nearly all small mammals fed to offspring during behavioral observations were red-backed voles (*Clethrionomys gapperi*; R. D. Dawson, unpubl. data), and so our index of prey abundance uses only vole numbers as opposed to all small mammals.

This index correlates well with variation in hatching asynchrony, sex ratios and cannibalism of nestlings, and egg sizes of kestrels on our study area (Bortolotti et al. 1991, Wiebe and Bortolotti 1992, 1994b, 1995).

EFFECTS OF WEATHER ON PARENTAL PROVISIONING AND OFFSPRING CONDITION

A permanent weather station located on the study area recorded ambient temperature, precipitation, and wind speed at hourly intervals throughout each field season. To obtain an index of overall weather "day type," we used the first component (PC1) of a principal components analysis. Data from all 3 years were used in the analysis, and input variables were mean daily temperature (°C) and wind speed (m sec^{-1}), and total amount (mm) and duration (hr) of precipitation. Temperature is expected to affect offspring condition and/or mortality at all times of the day, whereas wind speed, total precipitation, and duration of precipitation are likely to primarily affect parental provisioning rates. Therefore, mean daily temperature was calculated using the entire day (i.e., 24 hr), whereas mean wind speed, total precipitation, and duration of precipitation were calculated only for the hours between 06:00 to 22:00, corresponding approximately to the time when parent kestrels provisioned their young. The PC1 variable derived from our analysis produced a continuous distribution that at one extreme represented a cold, windy day with rainfall (positive PC1 values), and at the other extreme represented a warm, calm day without precipitation (negative PC1 values).

For each nest, PC1 values were averaged over the brood-rearing period (from 1 day post-hatch to 23 days old, just prior to fledging) to produce a variable that described the average weather conditions experienced by a nest. These average values were used to test for effects of weather on offspring condition and survival. For tests examining the effect of weather on parental provisioning, we used the PC1 describing the day type for the day the observation was made. In addition, we also examined the relationship between duration of rainfall and provisioning.

PARENTAL PROVISIONING

To quantify parental provisioning rates, we placed camouflaged video cameras (Hitachi VHS Model VM-3700A) approximately 5 to 15

m from kestrel nests. Nestling age ranged from 1 to 25 days during observation periods, and cameras were deployed at random times between 07:00 and 20:00. Once deployed, cameras were allowed to run the length of a video cassette and recorded all visits to the nest by adults during this time. Most parents visited nests immediately after cameras were set, and in many cases female parents were already present in the nest box at the start of observation periods. Observation periods where either parent appeared to be potentially disturbed by the camera were discarded. We also discarded observations that were less than 2 hr, as it has been shown previously that a minimum observation period of 2 hr is necessary to obtain estimates of provisioning rates that are not biased by the length of the sampling period (G. R. Bortolotti and R. D. Dawson, unpubl. data). Regardless, nearly all observations were the length of a video cassette, about 2.7 hr ($n = 73$).

We used two types of data in analyses. First, we quantified the number of trips parents made to the nest with prey. However, because selection of prey by parents may be altered by variation in brood demand or resource levels (Wright and Cuthill 1990), we also examined biomass brought to the nest. By using video observations, we were able to identify nearly all rodent prey to species, and other vertebrate prey and insects to Order. In addition, we estimated the size of prey brought to nests by measuring prey on the video monitor with calipers and comparing these measurements with objects of known size. Estimates of prey size were then used to calculate the biomass of prey delivered using length-mass relationships derived from a sample of representative prey captured with snap traps (mammals), sweep nets (invertebrates), or by measuring prey in kestrel boxes (birds and amphibians).

NESTLING SIZE AND MORTALITY

Kestrel eggs within a clutch generally hatch over a period of 1.5–3.5 days, and therefore siblings within a nest may differ in age (Wiebe and Bortolotti 1994b). Here, we use age to refer to the age in days of the oldest nestling within a brood. We measured body mass (nearest g) and length of the tenth primary feather (nearest mm) when the oldest nestling of the brood was 24 days old.

During visits to nests throughout brood rearing, we documented whether nestling mortality

had occurred since the last visit. Missing nestlings were assumed to have died and been removed from the nest box by parents or cannibalized by parents or siblings (Bortolotti et al. 1991) if they were too young to have left the nest on their own accord. For many nests where mortality occurred, we maintained a brood size of five by replacing dead nestlings with offspring from other nests that were not used in this study. Replacement nestlings were selected so that they were of the same age and within the range of body mass and tenth primary feather lengths that were present in the nest so that size hierarchies were not altered. If these criteria were not met, nests were discarded from further study, and so sample sizes vary among analyses.

STATISTICAL ANALYSES

We measured annual variation in weather in two ways. First, we compared day type (PC1) among years during the period of time between when the first nest used in our study hatched young and when the last nest fledged young, a period that varied from 49 to 50 days among years. Then, we examined the cumulative effects of weather at each nest by averaging the PC1 over the entire brood rearing period for each nest (see above), and comparing these values among years. Analysis of variance (ANOVA) was used to test for annual differences in both weather and vole numbers. When significant differences were detected, multiple range tests using a Bonferroni-corrected alpha value were employed in pairwise comparisons.

To test for relationships between natural food supply and parental provisioning, we used data collected when offspring were between 16 and 25 days old. We chose this period because prey delivery rates were relatively constant across this range of ages, and they are among the highest that occur during the nestling period (Wiebe and Bortolotti 1994a), which maximizes the probability of detecting significant effects if they existed. When more than one observation from an individual nest appeared in the data set, the mean value for that nest was used. To meet assumptions of normality, prey delivery rates were transformed ($\ln [\text{prey hr}^{-1} + 1]$) before analysis.

For all analyses of provisioning rates, we also entered hatching date and nestling age in our models as potential covariates. In no case did these variables contribute significantly to our statistical models; therefore, each was iteratively

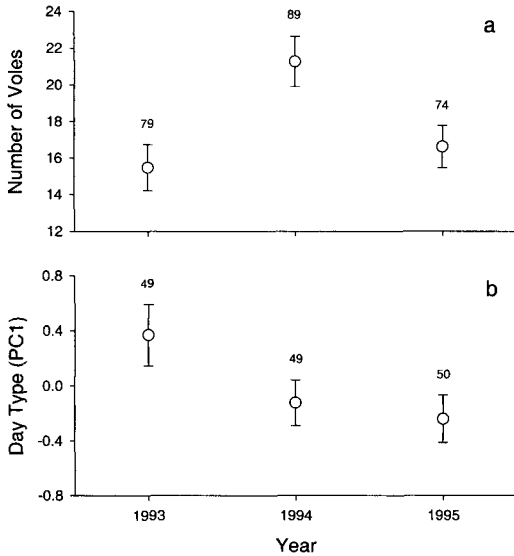


FIGURE 1. (a) Mean \pm SE number of voles trapped on territories of American Kestrels from 1993 to 1995. Vole numbers were standardized to represent the number of animals per 100 trap nights. Number of territories trapped is indicated above error bars. (b) Mean \pm SE day type experienced by nestling American Kestrels over the course of the brood rearing period between 1993 and 1995. Sample sizes above error bars refer to the number of days during each year that chicks were in nests, and so represents the period from hatching of the first nestling of the season to when the last nestling of the season fledged. Large positive values for day type represent inclement weather.

removed and analyses repeated. Because we detected annual variation in both vole numbers and average day type (see below), we tested whether prey and biomass delivery rates showed similar yearly variation using ANOVA. Pearson correlations were used to test for relationships between delivery rates and vole numbers on territories or average day type. In addition to day type, we also tested whether rain alone was related to delivery rates.

We tested for annual variation in body mass and tenth primary length of nestlings with ANOVA, and investigated relationships between these measures of size and vole numbers or day type using Pearson's correlations. Kestrels are sexually dimorphic in size as nestlings, so we calculated means for body mass and primary length of males and females separately for each nest. Subsequently, the sexes were analyzed separately rather than using sex as a factor, to avoid any nest appearing more than once in analyses.

We used two approaches to test for effects of food abundance or weather on nestling mortality. First, each nest was classified according to whether or not any nestlings died before fledging (i.e., prior to 24 days of age) and G -tests were used to investigate whether annual variation existed. We then used logistic regression with probability of a nest experiencing mortality (yes/no) as the dependent variable, and vole numbers and day type as explanatory independent variables. Second, for each nest we measured the proportion of young dying by calculating the ratio of number of nestlings that died to the total number in the nest between ages 1 and 24 days. We tested for annual differences in the proportion of nestlings dying within nests using a Kruskal-Wallis ANOVA. Spearman's correlation was used to test for significant relationships between vole numbers or day type and proportion of nestlings within nests dying before 24 days of age. Preliminary analyses of nestling size and mortality also used hatching date as a potential covariate; however, this variable was not significant in any analysis and so was not considered further.

Statistical analyses were performed using SPSS (Norušis 1993). All tests are two-tailed, and means are presented \pm SE.

RESULTS

ANNUAL VARIATION IN FOOD ABUNDANCE AND WEATHER

Vole numbers differed significantly among the three years of study ($F_{2,239} = 6.0$, $P < 0.01$; Fig. 1). Multiple range tests showed that voles were more abundant in 1994 than in either 1993 or 1995 ($P < 0.05$), but that 1993 and 1995 were not significantly different. There was a trend for weather during brood rearing to differ among years, but not significantly so ($F_{2,145} = 2.9$, $P = 0.058$; Fig. 1). However, when we considered the cumulative effects of weather by averaging day types for each nest from hatching to fledging, there were significant annual differences ($F_{2,32} = 178.5$, $P < 0.001$). This annual variation in weather was largely attributable to annual differences in the duration of rainfall; broods hatching in 1993 experienced on average 71.9 ± 2.9 hr ($n = 11$) of rain from hatching to fledging, those in 1994 were subjected to 33.4 ± 0.7 hr ($n = 9$), whereas broods in 1995 experienced only 16.4 ± 0.6 hr ($n = 15$) of rain.

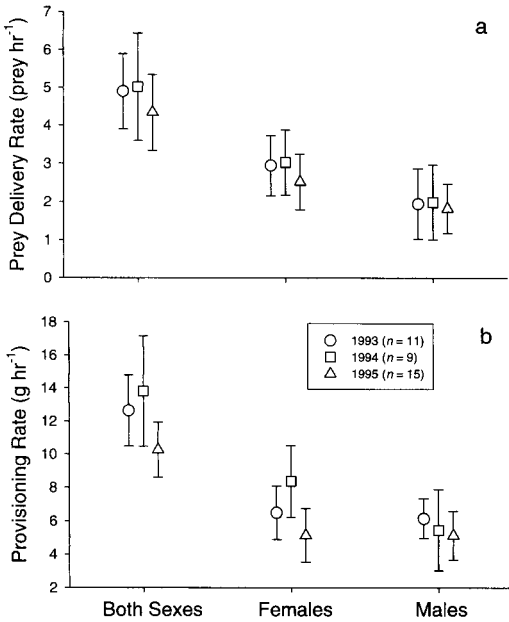


FIGURE 2. Prey (a) and biomass (b) delivery rates per hour \pm SE made to nests by American Kestrels from 1993 to 1995 when nestlings were between 16 and 25 days old. Sample sizes refer to number of nests.

EFFECTS OF FOOD SUPPLY AND WEATHER ON PARENTAL PROVISIONING

The number of prey items and biomass brought to nests by both parents, and each sex separately, was comparable in all 3 years ($F_{2,32} < 0.7$, all $P_s > 0.40$; Fig. 2). We detected no significant correlation between vole numbers on territories and either the number of prey items delivered per hour ($r = -0.01$, $n = 35$, $P = 0.99$) or the biomass of prey delivered per hour ($r = -0.03$, $n = 35$, $P = 0.86$). Considering only vertebrate prey delivered to nests, there also was no significant correlation between vole numbers on territories and either number of prey items ($r =$

0.15 , $n = 35$, $P = 0.38$) or biomass ($r = 0.05$, $n = 35$, $P = 0.78$) delivered per hour.

Weather during the day of the observation period was not correlated with number of prey items ($r = -0.08$, $n = 35$, $P = 0.65$) or biomass ($r = -0.01$, $n = 35$, $P = 0.94$) delivered per hour. Due to technical limitations of operating video equipment when it was raining, we have few data to adequately test for effects of adverse weather on adult provisioning rates. However, during 1993 when rain was frequent, parent kestrels brought fewer prey items (2.3 ± 0.7 prey hr^{-1}) to nests during observation periods with rain (median = 94.4 min of rainfall, range 17–164 min, $n = 5$ observation periods) than during observations when no rain was detected (5.9 ± 0.8 prey hr^{-1} ; $F_{1,24} = 8.9$, $P < 0.01$). There also was a trend for less biomass to be delivered during observations with rain (7.6 ± 2.6 g hr^{-1}) than during those observations when no rain was detected (13.9 ± 1.4 g hr^{-1} ; $F_{1,24} = 4.1$, $P = 0.053$). Using all observations where rain was detected, biomass delivered per hour declined significantly with the number of minutes of rainfall during the observation period ($r = -0.68$, $n = 10$, $P = 0.03$). A similar but nonsignificant relationship was found between number of prey items delivered per hour and minutes of rain ($r = -0.43$, $n = 10$, $P = 0.23$).

EFFECTS OF FOOD SUPPLY AND WEATHER ON OFFSPRING SIZE AND MORTALITY

There were no annual differences in body mass of either female or male kestrels at fledging; however, significant annual differences in tenth primary length at fledging were detected for both sexes (Table 1). Multiple range tests showed that primary lengths were significantly different ($P < 0.05$) between 1993 and 1995 for both sexes of nestling (Table 1). Vole numbers

TABLE 1. Annual variation in mean (\pm SE) body mass (g) and tenth primary lengths (mm) of nestling American Kestrels at 24 days old (minimum fledging age) in broods of five nestlings. Sample sizes are in brackets and refer to the number of nests.

Year	Males		Females	
	Mass	Tenth primary	Mass	Tenth primary
1993	109.5 \pm 3.9 (7)	51.0 \pm 3.5 (7)	118.1 \pm 3.4 (8)	55.6 \pm 2.0 (8)
1994	112.2 \pm 3.2 (8)	58.4 \pm 2.6 (8)	122.3 \pm 1.9 (8)	61.4 \pm 2.2 (8)
1995	115.2 \pm 1.3 (15)	63.8 \pm 1.9 (15)	125.2 \pm 1.6 (15)	63.6 \pm 1.9 (15)
<i>F</i> (df)	1.38 (2, 27)	6.37 (2, 27)	2.69 (2, 28)	3.79 (2, 28)
<i>P</i>	0.27	0.005	0.09	0.03

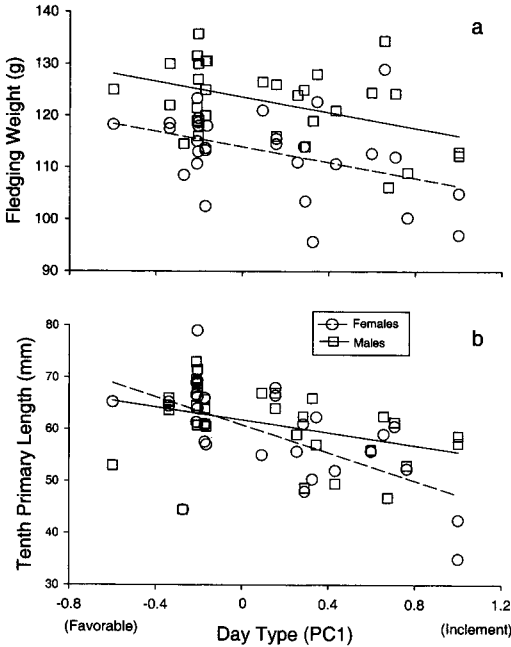


FIGURE 3. The decline in (a) fledging mass (females: $r = -0.44$, $n = 31$, $P = 0.01$; males: $r = -0.41$, $n = 30$, $P = 0.02$), and (b) tenth primary lengths (females: $r = -0.37$, $n = 31$, $P = 0.04$; males: $r = -0.63$, $n = 30$, $P < 0.01$) of nestling American Kestrels as the average weather (day type) experienced during brood rearing became more inclement.

did not correlate significantly with fledging mass or tenth primary lengths of either female ($n = 31$, mass: $r = -0.10$, $P = 0.59$; tenth primary: $r = 0.10$, $P = 0.59$) or male ($n = 30$, mass: $r = -0.02$, $P = 0.93$; tenth primary: $r = -0.04$, $P = 0.85$) nestlings. Nestlings of both sexes fledged at lighter weight and with shorter tenth primaries as the average weather they were exposed to during brood rearing became more inclement (Fig. 3).

When nests were classified according to whether or not offspring mortality occurred, there were large differences in mortality among years ($G_2 = 29.7$, $P < 0.001$; Fig. 4), with mortality highest in 1993 and lowest in 1995. The proportion of nestlings dying in nests also differed in a similar manner among years (Kruskal-Wallis ANOVA, $\chi^2_2 = 15.3$, $P < 0.001$). Multiple comparisons showed significant differences ($P < 0.05$) between 1993 and 1995 in the proportion of offspring within nests experiencing mortality.

The probability of mortality occurring within

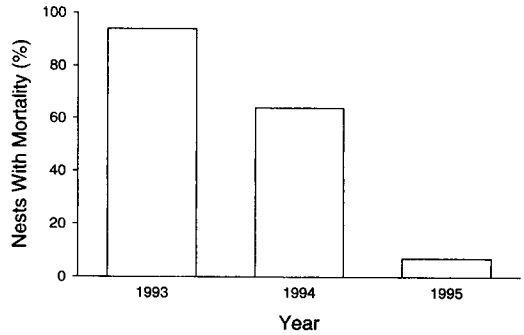


FIGURE 4. Percentage of nests where at least one nestling American Kestrel died prior to 24 days of age (minimum fledging age) from 1993 to 1995.

a nest increased as weather became more adverse (logistic regression, $\chi^2_1 = 11.8$, $P < 0.001$; Fig. 5), but was unaffected by the number of voles present on the territory ($\chi^2_1 = 0.1$, $P = 0.71$). Similarly, the proportion of offspring within nests dying before fledging increased as weather became more inclement ($r_s = 0.60$, $n = 34$, $P < 0.001$), but was unrelated to vole numbers ($r_s = 0.03$, $n = 34$, $P = 0.85$).

DISCUSSION

PARENTAL PROVISIONING RATES

Life-history theory suggests that parents should be prudent in their allocation of energy to provisioning offspring (Drent and Daan 1980). During years when prey is abundant, parents will be able to provide more food per unit of energy

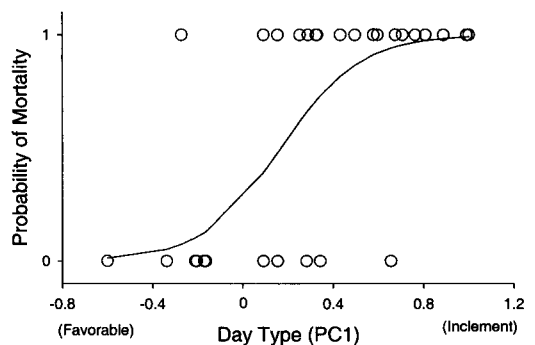


FIGURE 5. Increased probability of mortality occurring within nests of American Kestrels as the average weather (day type) experienced by nestlings becomes more inclement. Mortality is defined as either 0 (no nestlings within a nest dying) or 1 (at least one nestling dying). The regression line was fitted using a logistic regression ($P < 0.001$). Large values for day type represent inclement weather.

expenditure than during poor food years. As a result, annual variation in parental provisioning should mirror variation in food abundance. However, despite annual differences in vole abundance during our study (Fig. 1), we could find no difference among years in the number of prey or biomass delivered to nests by parent American Kestrels (Fig. 2). Our results are similar to those previously reported for American Kestrels by Gard and Bird (1990). In addition, we found no significant correlations between vole numbers on territories and prey deliveries by parents on those territories.

Although our results suggest that the abundance of prey had little effect on parental provisioning behavior of American Kestrels on our study area, other studies have demonstrated the importance of food abundance in determining reproductive performance of birds of prey. For example, annual variation in reproductive success of Eurasian Kestrels (*Falco tinnunculus*) is closely tied to vole abundance (Korpimäki and Wiehn 1998). Similarly, Hakkarainen and Korpimäki (1994) showed that Tengmalm's Owls (*Aegolius funereus*) in Finland provisioned according to offspring survival prospects which are determined by population cycles of voles. On our study area (Fig. 1; Wiebe and Bortolotti 1994b), however, voles do not show the predictable and extreme cycles of population density that occur in Finland (Korpimäki and Wiehn 1998) and it seems doubtful that American Kestrels were altering their provisioning strategies in response to variation in probability of offspring survival mediated through vole population cycles. Instead, voles may have been sufficiently abundant on our study area to support successful reproduction, and the small variation in numbers that we detected did not have appreciable effects on provisioning behavior of American Kestrels.

Using a composite measure of weather (PC1), we found no compelling evidence that weather patterns affected prey provisioning by kestrels. Our tests for the general effect of weather on provisioning are probably weak as we were unable to actively record parental behavior during periods of rain. Our results do suggest, however, that across the range of variation in weather that might be considered reasonably favorable, weather had little effect on provisioning rates. Highly inclement weather appeared to have large effects; the few data collected during ob-

servation periods experiencing rain showed that prey delivery rates declined significantly as the duration of the period of rain increased.

There is abundant evidence that inclement weather directly affects both hunting effort and prey deliveries to nests of a wide variety of species (Rijnsdorp et al. 1981, Simmons 1986, Veistola et al. 1997). Such results are probably due to inclement weather, in particular rain, reducing the activity of prey (Olsen and Olsen 1992). Voles may reduce or cease activity during wet, cold weather (Lehmann and Sommersberg 1980). In addition, both abundance and availability of insects also is dependent on weather (Rodenhouse and Holmes 1992). Severe weather probably results in a reduction in availability of all prey types that kestrels use, as opposed to simply causing a shift in the type of prey consumed as is commonly seen in birds under stress (Wright and Cuthill 1990).

SIZE AND SURVIVAL OF NESTLINGS

Although growth of nestling birds is often affected by food abundance (Moss 1979, Gebhardt-Henrich 1990), weather had a larger effect on size and survival of nestling kestrels than did prey abundance. We found that tenth primary lengths of both sexes at fledging differed significantly between 1993 and 1995 (Table 1), years that had similar numbers of voles, but significantly different weather during brood rearing (Fig. 1). Although we could not detect annual variation in fledging mass of kestrels, the patterns were similar to tenth primary lengths (Table 1). Moreover, both body mass and tenth primary length at fledging declined significantly as the average weather experienced by broods became increasingly inclement (Fig. 3); no significant correlations between vole numbers and size of nestlings at fledging existed.

Reductions in offspring growth associated with poor weather may result from either direct or indirect effects (Siikimäki 1996). Direct effects occur when energy expenditure for thermoregulation is increased as a result of chilling of nestlings (Tinbergen and Dietz 1994), whereas indirect effects result from decreased provisioning by parents during inclement weather (see above). In addition to depressing prey availability, harsh weather may also force female parents to spend more time brooding young, and so further reduce the amount of food brought by parents to nests. Regardless of whether effects

were direct or indirect, our results suggest that kestrels exposed to inclement weather probably suffered chronic as opposed to acute food shortages, as short-term food deprivation is unlikely to have lasting effects on nestling morphology (Negro et al. 1994).

In addition to variation in offspring size at fledging, there was also significant annual variation in the number of nests experiencing mortality (Fig. 4), as well as in the proportion of nestlings within nests that died. As with feather lengths, variation in mortality among years mirrored patterns of weather, but not vole abundance (Fig. 1). The probability of a nest experiencing mortality increased as average day type became more inclement (Fig. 5), but vole abundance had no effect. Similarly, the proportion of offspring within nests dying before fledging also increased as day type became more severe, but was not related to vole numbers. Again, the apparent unimportance of prey abundance in determining nestling survival and size is probably due to voles being sufficiently numerous to support successful reproduction. Our results are consistent with previous studies that showed low fledgling production in years with continuous rain and low temperatures (Aparicio 1997, Weimerskirch et al. 1997). Weather-induced mortality, like effects of weather on growth, can arise from direct or indirect effects, but most studies have implicated indirect effects through starvation as being most important (Siikimäki 1996, Veistola et al. 1997).

CONCLUSIONS: FOOD LIMITATION IN AMERICAN KESTRELS

Overall, the evidence presented in this study suggests that American Kestrels breeding on our study area are limited by food. Our results further suggest that provisioning behavior of kestrels raising offspring is not proximally constrained by the abundance of food but rather by the availability of food, mediated through variation in weather. Whereas the results from our observations of provisioning are not conclusive due to the limitations of the data set, results for effects of variation in weather on reproductive success are clear; nests experiencing unfavorable weather during brood rearing were more likely to suffer brood reduction, and the proportion of young within such nests dying prior to fledging was higher. Additionally, nestlings that experienced unfavorable weather during brood

rearing fledged at lighter weights and with shorter primaries. Condition of nestling passerines at fledging is thought to reflect their future survival probabilities (Merilä and Wiggins 1995). Kestrels that fledge in poor condition may have reduced fat reserves (Lacombe et al. 1994) and so it is reasonable to assume that offspring condition at fledging reflects survival probabilities. It will be important for future researchers studying food limitation in birds to not only quantify prey abundance, but also control for factors that may influence availability, such as weather.

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