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Experimental evidence for food limitation and sex-specific strategies of American kestrels (*Falco sparverius*) provisioning offspring

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Abstract For birds with altricial young, the brood-rearing period is one of the most energetically expensive periods in their lives and may be the bottleneck for fitness. Because parents are expected to be prudent in allocating resources between reproduction and self-maintenance, food supply should be an important factor determining reproductive decisions during brood rearing. Parents with abundant food are expected to have enhanced fitness because they are able to reduce their work rates and increase their own survival chances, because their offspring may be of higher quality, or some combination of these. However, few studies have simultaneously documented all of these variables in a single investigation. We performed a food supplementation experiment to test how food supply influenced provisioning decisions by parent American kestrels (*Falco sparverius*). Female kestrels showed a strong response to extra food and reduced their provisioning rates. As a result, supplemented females had higher return rates than control females, suggesting significant effects of food on female survival. Because females used extra food to increase their fitness, our results suggest that kestrels raising offspring are limited by food. Male kestrels whose nests were supplemented also responded to extra food by reducing provisioning, but to a much lesser extent than their mates. Male parents did not appear to benefit from supplementation, as their return rates were similar to control males. The total amount of food received on a daily basis by nestlings was similar between supplemented and control nests. Supplemented offspring therefore did not fledge in

better condition or have higher survival rates than control nestlings; the only significant factor consistently affecting offspring condition and survival was weather.

Keywords American kestrels · Offspring quality and survival · Prey abundance · Provisioning · Supplemental food

Introduction

Food supply is thought to be one of the most important factors limiting reproductive success of birds (Lack 1947; Martin 1987, 1995). Indeed, supplementation experiments have shown that increased availability of food may result in earlier clutch initiation dates, larger egg and occasionally larger clutch sizes, enhanced growth and survival of offspring, or higher survival of parents (Martin 1987; Meijer et al. 1988; Korpimäki 1989; Boutin 1990; Simons and Martin 1990; Wiebe and Bortolotti 1995a, b; Wiehn and Korpimäki 1997; Korpimäki and Wiehn 1998). However, making generalizations from such results is difficult because there has been much variation among studies in the amount and duration of feeding. For example, studies that have supplemented food through the entire breeding season (Hochachka and Boag 1987; Arcese and Smith 1988; Kelly and Van Horne 1997) are unable to distinguish during which period of the reproductive cycle food limitation occurs. Similarly, providing supplemental food only prior to egg laying generally cannot test whether food also is limiting during the nestling period (Ward and Kennedy 1996).

Relatively few studies have provided extra food from hatching to fledging (Wiehn and Korpimäki 1997), despite the fact that brood rearing is an energetically expensive period for birds raising altricial young, and may be the bottleneck for fitness (Drent and Daan 1980). Adequate provisioning of offspring is obviously beneficial for parents because such behaviour ensures offspring quality and survival (Roff 1992; Stearns 1992). However, provisioning is also costly because it may reduce sur-

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vival and future reproduction of parents (Williams 1966; Drent and Daan 1980; Lindén and Møller 1989). Therefore, the response of parents when extra food is provided to their offspring will depend on how they choose to balance these costs and benefits (Roff 1992; Stearns 1992). At one extreme, if parents have the ability to alter their behaviour in response to supplemental feeding, they may choose to retain the benefits of extra food for themselves and reduce their provisioning rate. Because the costs incurred by parents will be reduced, it is expected that their survival will be enhanced, but offspring quality and survival will be similar to that at unfed nests. At the other extreme, parents may have fixed investment strategies and be either unwilling or unable to modify their behaviour in response to supplemental food, such as occurs in some seabirds where provisioning is determined by an intrinsic parental rhythm and not by nutritional needs of the offspring (Hamer and Hill 1994; references in Bolton 1995). In these cases, when provided with supplemental food, provisioning rates and costs of reproduction may remain unchanged; however, offspring quality and survival will be enhanced.

Most researchers have assumed that if food is limiting during brood rearing, then parents would use supplemental food to increase their fitness (Simons and Martin 1990). While fitness can be enhanced through increased survival and quality of young in the current breeding attempt, or increased survival of parents (above), few studies have simultaneously documented all of these variables in a single investigation. Moreover, supplementation is thought to be beneficial only when natural food supplies are a poor (Dewey and Kennedy 2001), yet most previous studies have not quantified natural abundance of prey (notable exceptions include Wiebe and Bortolotti 1995a; Wiehn and Korpimäki 1997). We performed a food supplementation experiment to test whether reproduction of the American kestrel (*Falco sparverius*) is limited by food during the brood-rearing period. Kestrels are small, monogamous falcons that are widely distributed throughout North America (Bird 1988). Kestrels are known to use a diversity of prey species, but in our study area in north-central Saskatchewan their main prey is small mammals (Bortolotti et al. 1991), primarily red-backed voles (*Clethrionomys gapperi*; Dawson 1999). We quantified small mammal numbers during this study, allowing us to put the results of our supplementation experiment into perspective with abundance of natural prey.

Nestling American kestrels frequently die of starvation (Dawson and Bortolotti 2000), leading Wiebe and Bortolotti (1995a) to suggest that kestrels were normally limited by food availability during brood rearing. Previous research on our study population has also shown that food supply affects variation in hatching asynchrony, sex ratios and cannibalism of nestlings, and egg sizes of kestrels (Bortolotti et al. 1991; Wiebe and Bortolotti 1992, 1994, 1995b). Therefore, given that kestrels appear to react to variation in food supply by facultatively manipulating many components of reproduction, we expected

that kestrels would respond strongly to our manipulation. Specifically, we predicted that parents would alter their behaviour when their nests were supplementally fed, and reduce their provisioning rates. Furthermore, we expected that the effects of supplemental food on provisioning strategies would be sex-specific. Kestrels have distinct sex roles during brood rearing, with males providing most of the food until the young are about 10 days of age. Males transfer food to their mates who feed the young as well as brood offspring and guard the nest (Balgooyen 1976; personal observation). We investigated whether parents shared the benefits of supplemental food equally, or whether one sex was more likely to take advantage of the experimentally increased food supply. We predicted that because females spend more time at nests and so have more access to supplemental food, particularly during the early stages of brood rearing, that they would respond more strongly to the manipulation than their mates (see also Wiehn and Korpimäki 1997). Additionally, females are larger than males, and possibly better able to monopolize extra food at the nest.

Methods

We studied a population of American kestrels breeding in nest boxes from 1993 to 1995 near Besnard Lake, Saskatchewan (55°N, 106°W). Our study area encompassed an extensive network (approximately 300 km) of gravel roads and logging trails (see map in Dawson and Bortolotti 1999). 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 (Bortolotti 1994). Kestrels arrived on our study area in mid-to late-April, and egg laying commenced in mid-May. We visited each nest box every 3–4 days from mid-May to mid-June, or until the first egg was laid. Clutch size was determined by revisiting nests again after laying was complete. Our study used only nests that had five eggs, the modal clutch size for our population (Tella et al. 2000), which eliminated any potential effects that clutch size may have had on parental behaviour or nestling quality. Although the majority of nests in this study hatched five young, some nests experienced partial hatching failure. In these cases, we added foster young from nests not used in this study to maintain a brood size of five nestlings. A brood size of five probably also represents the maximum number of young that kestrels in our area can raise. Few pairs lay more eggs (only 1.2% of clutches have six eggs, none are larger; Tella et al. 2000) and between 1993 and 1997, only one pair was ever successful in raising six young (Dawson and Bortolotti, unpublished data).

Supplemental feeding

We randomly assigned each nest to either a treatment or control group. Supplemental food was provided to treatment nests from hatching until fledging (about 24–25 days old). Dead laboratory mice (*Mus musculus*) were placed, usually every 2 days, inside the nest box through the nest box hole using a telescoping pole to minimize disturbance. We varied the quantity of food provided throughout the nestling period so that the amount provided would approximately equal the daily energy requirements of a single nestling kestrel (Anderson et al. 1993). Through direct observations and the presence of white fur in pellets remaining in nest boxes, we were confident that supplements were being consumed. The sample of nests where no extra food was provided served as controls; these nests are the same as those studied by Dawson and Bortolotti (2000).

Provisioning rates

Parental effort of kestrels was estimated using provisioning rates to nests. We placed video cameras approximately 5–15 m from nests at random times between 0700 and 2000 hours CST, and recorded all visits to the nest by adults. Cameras were deployed on multiple days at each nest (see below) when nestlings were between 1 and 24 days old. During each observation period at a nest, cameras were allowed to run the length of a video cassette (2.71 h). 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. Data from observation periods where either parent appeared to be potentially disturbed by the camera were discarded.

Using video cameras to record observations allowed us to obtain two types of data for analysis (see also Dawson and Bortolotti 2000). First, we quantified the number of trips parents made to the nest with prey. We were also able to identify nearly all rodents to species, and other vertebrate prey and insects to at least the level of order. By measuring prey on the video monitor with callipers and comparing these measurements with objects of known size, we were able to estimate the size of prey brought to nests. These estimates of 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; see below), sweep nets (invertebrates), or by measuring prey in nest boxes (birds and amphibians). Supplemented mice that were delivered from food caches outside of the nest box were not included in the calculation of these prey delivery rates. We were also able to document the number, type and biomass of prey removed from nests, as well as the amount of time spent in nest boxes, by parents. Finally, we calculated the average biomass each nest received per day. Assuming that kestrels provision for the 16 h per day of daylight in our area, total daily biomass = (biomass delivered per hour – biomass removed hour) \times 16. For supplemented nests we also added to this value the mass of extra food that we provided each day.

Return rates

We used return rates to test whether supplemental food had consequences for survival of parents. From 1993 to 1995, we trapped adult kestrels during pre-laying using bal-chatri traps (Berger and Mueller 1959), and in nest boxes by hand during incubation. Each bird was given a unique combination of one aluminum and three coloured plastic leg bands. Return rates of adults were determined by recapturing kestrels on our study area from 1994 to 1997 using these same methods.

Quality and survival of offspring

Mass or size of offspring at fledging is thought to reflect quality because these variables influence probability of surviving to adulthood (Tinbergen and Boerlijst 1990; Magrath 1991). We documented the quality of nestling kestrels at fledging by measuring their mass (nearest gram) and tenth primary length (nearest millimetre) at 24 days old. We were able to accurately determine gender of each nestling because kestrels show sexual dimorphism in plumage as young as 8 days of age (Dawson, unpublished data; see also Bird 1988). In addition, during each visit to a nest throughout brood rearing we noted whether nestling mortality had occurred since the last visit. For nests where mortality did occur, we maintained a brood size of five by replacing dead nestlings with offspring from other nests that were not part of this study. If we were unable to obtain replacement nestlings and maintain a brood size of five, the nest was discarded from further study.

Both quality and mortality of nestling kestrels are significantly affected by weather experienced during brood rearing (Dawson and Bortolotti 2000). A permanent weather station located on our study area recorded ambient temperature, precipitation and wind

speed at hourly intervals throughout the field season. As a measure of weather conditions for each day we used the first component (PC1) of a principal components analysis that had mean daily temperature ($^{\circ}$ C) and wind speed (m/s), and total amount (mm) and duration (h) of precipitation as input variables. 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 only affect parental provisioning rates. Therefore, mean daily temperature was calculated using the entire day (i.e., 24 h), whereas mean wind speed, total precipitation and duration of precipitation were calculated only for the hours between 0600 and 2200 hours CST, corresponding approximately to the time when parents are provisioning young. PC1 from this analysis is a continuous variable where positive values represent cold, windy days with rainfall lasting many hours, while negative values were warm, calm days without precipitation. 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 called “day type” that described the average weather conditions experienced by a nest (details in Dawson and Bortolotti 2000).

Natural food abundance

We assessed abundance of food on territories of kestrels by censusing their main prey, 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 territories near nest boxes. At each station two snap traps were baited with peanut butter. Each line operated for 3 days, and traps were reset each morning. Data were standardized to mean number of animals per 100 traps nights. Most mammalian prey fed to offspring during behavioural observations were red-backed voles (92%; Dawson 1999 and unpublished data); however, in our analyses we used numbers of all small mammals because our results were the same regardless of whether numbers of small mammals or only numbers of voles were used. Moreover, using numbers of all small mammals allowed us to directly compare food abundance during our study to that of Wiebe and Bortolotti’s (1995a) study.

Statistical analysis

From the perspective of nestlings, the total amount of food delivered is an important factor determining their growth and survival. We therefore tested whether behaviour of parent kestrels was influenced by food supplementation using provisioning data for both sexes combined. Differences in provisioning were tested with ANOVA that used treatment (control, supplement) and year as independent variables and either number or biomass of prey delivered per hour as the dependent variable. We also tested whether each sex of parent responded similarly to food supplementation using repeated-measures ANOVA. Our between-subjects factors were treatment and year, while the within-subjects factor was sex of parent. Separate analysis were performed for the number of prey items and biomass delivered per hour. We further tested how supplementation affected provisioning using, for each sex separately, ANOVA with treatment and year as independent variables and provisioning (number or biomass) as the dependent variable. We also compared the contribution of each sex to parental care within nests using paired *t*-tests.

For all analyses of provisioning (number and biomass delivered), we used data from the period when offspring were between 11 and 24 days old. We limited our analyses to these ages because prior to this, provisioning data are complicated by the different sex roles of parents. From hatching until young are about 10 days old, most of the prey brought to nests is delivered by the female parent, but the vast majority of prey is actually captured by the male parent (Balgooyen 1976; personal observation). Once offspring are older than 10 days, female parents begin to hunt for their broods.

If two or more observations from the same nest occurred in the data set, the mean value for the nest was used.

To investigate whether supplementation affected prey removal rates or time spent in nest boxes by parents, we used data from the entire nestling period in a series of repeated measures ANOVA. Our between-subjects factors were treatment (control or supplement) and year, while the within-subject factor was stage of nestling period (early or late). Observations were considered as being during the early stage of the nestling period if they occurred when offspring were between 1 and 10 days old, and during the late nestling period if they occurred when young were between 11 and 24 days old. For a nest to be included in these analyses, it was necessary that observations were carried out during both early and late stages. Due to logistical constraints and naturally occurring brood reduction, observations were not made at all nests during both stages. If two or more observations from the same nest and same age period occurred in the data set, the mean value for the nest during the age period was used.

We used adult return rates to test for effects of food supplementation on adult survival; however, because return rates of adult kestrels were low, we pooled data from all 3 years in analyses to increase statistical power. For each sex separately, we tested whether there were differences in return rates of adults between control and supplemented nests using G tests. Among birds that returned, we also tested whether dispersal distance, defined as the distance (km) between the nest location during this experiment and the nest location in subsequent years, varied between the sexes and between treatment using ANOVA. To meet assumptions of normality, dispersal data were ln-transformed before analysis. In two cases, birds were used twice in our experiment (one male and one female, both had supplemented nests in one year and then served as controls in the second year). To avoid pseudoreplication we used only the first observation for both of these birds.

To test for effects of food supplementation on mass and length of tenth primary of nestlings at fledging, we used average day type experienced by a brood as a covariate in analysis of covariance, with treatment and year as independent variables. Kestrels show sexual size dimorphism as nestlings (Dawson and Bortolotti 1999), so we calculated means for mass and length of tenth primary of males and females separately for each nest. Subsequently, to avoid any nest appearing more than once in analyses, the sexes were analysed separately rather than using sex as a factor. We tested whether supplemented and control nests differed in their probability of at least one nestling dying before 24 days of age using a logistic regression model with occurrence of mortality (yes/no) as the dependent variable, treatment as a categorical variable and day type as a covariate.

For all analyses, if interactions or year effects did not approach significance ($P > 0.10$), they were iteratively removed from the models and analyses redone. Furthermore, analyses of provisioning initially included as covariates the age in days of nestlings and time of day observations were made; however, because these variables were never significant, they were dropped from final models. Analyses were performed using SPSS (Norušis 1993) and SAS (SAS Institute 1990), and all tests are two-tailed and we considered results significant at $P < 0.05$. Means are presented \pm SE, and were calculated using the least-square means option of PROC GLM (SAS Institute 1990).

Results

Abundance of natural prey

There was significant annual variation in prey abundance during the brood-rearing period ($F_{2,252} = 6.56$, $P = 0.002$). A posteriori tests (Tukey's HSD) showed that small mammal numbers on trap lines were significantly higher in 1994 (21.3 ± 1.2 animals/100 trap nights, $n = 79$ territories) than either 1993 (15.5 ± 1.3 , $n = 89$ territories;

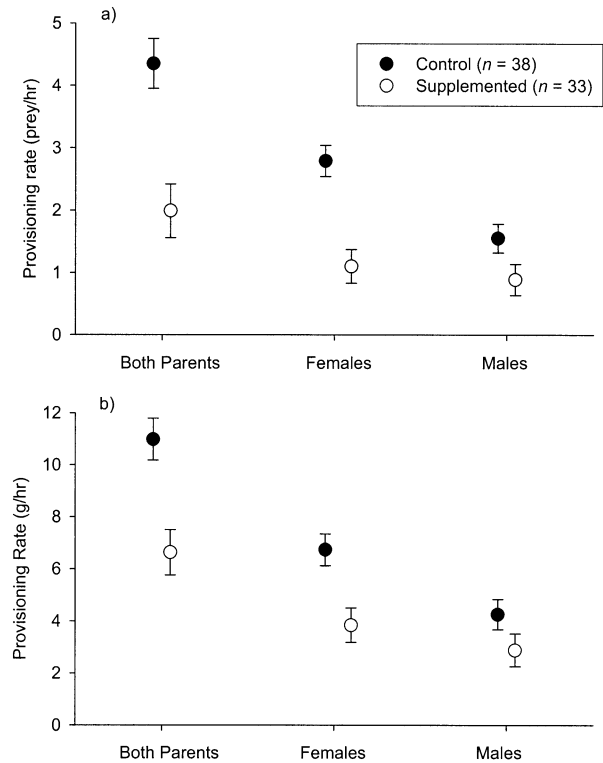


Fig. 1 Number of **a** prey and **b** biomass (\pm SE) brought by American kestrels (*Falco sparverius*) to control and food-supplemented nests by both parents, female parents, and male parents when nestlings were between 11 and 24 days old

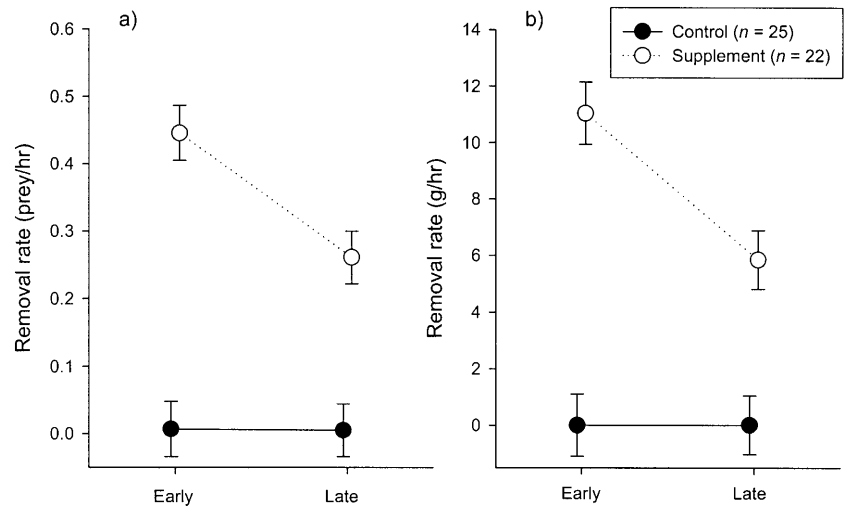
$P = 0.003$) or 1995 (16.2 ± 1.2 , $n = 87$ territories; $P = 0.01$), but no differences existed between 1993 and 1995 ($P = 0.91$).

Behaviour and return rate of parents

Over the course of the study 37 nests were supplemented with food during brood rearing and 43 nests served as controls. There were no differences between supplemented and control nests in hatching date, weather during brood rearing, or hatching success (all P values > 0.65). Provisioning data were collected at 33 supplemented (1993: $n = 11$, 1994: $n = 8$, 1995: $n = 14$) and 38 control nests (1993: $n = 14$, 1994: $n = 9$, 1995: $n = 15$). Number of observation periods averaged 2.6 ± 0.1 per nest for an average of 7.0 ± 0.4 h of observation per nest. Considering the contributions of both sexes combined, parents whose nests were supplemented with food delivered significantly fewer prey items than control parents ($F_{1,69} = 16.22$, $P < 0.001$). Similar results were obtained for the amount of biomass delivered; parents with supplemented nests delivered less biomass than control parents ($F_{1,69} = 13.40$, $P < 0.001$; Fig. 1).

Repeated measures ANOVA revealed that female parents delivered significant more prey items than did their mates did ($F_{1,69} = 12.79$, $P < 0.001$), and that supplemented parents delivered significantly fewer prey than did

Fig. 2 Number of **a** prey and **b** biomass (\pm SE) removed by female American kestrels from control and food-supplemented nests during early (nestling age 1–10 days old) and late (nestling age 11–24 days old) stages of brood rearing



control parents ($F_{1,69}=16.20$, $P<0.001$; Fig. 1). Additionally, there was a significant sex by treatment interaction ($F_{1,69}=6.62$, $P=0.01$), suggesting that food supplementation did not alter the provisioning behaviour of each sex of parent equally. Indeed, when we analysed data for each sex separately with ANOVA, we found that supplemented females significantly reduced the number of prey delivered compared to control females ($F_{1,69}=21.54$, $P<0.001$), but the effect of supplementation on number of prey delivered by males was not significant ($F_{1,69}=3.68$, $P=0.06$). Results from repeated measures analyses for biomass delivered per hour were similar to those for number of prey; female parents delivered significantly more biomass than did males ($F_{1,69}=7.08$, $P=0.01$), and supplemented parents delivered significantly less biomass than control parents ($F_{1,69}=12.78$, $P<0.001$; Fig. 1). However, we did not detect a significant sex by treatment interaction ($F_{1,69}=1.38$, $P=0.24$), even though our separate analyses by sex showed a significant effect of supplementation on biomass delivered by females ($F_{1,69}=10.27$, $P<0.001$), but no differences between supplemented and control males ($F_{1,69}=2.57$, $P=0.11$; Fig. 1). Considering the contributions of each sex within nests, females delivered more prey items and biomass than their mates in control nests, but there were no differences between the sexes in food-supplemented nests (Table 1), suggesting that supplementation allowed females to reduce provisioning rates.

Over the entire brood rearing, we observed 86 instances where prey were removed from nests by parents. Males were responsible only once (1.2%); therefore, subsequent analyses consider only prey removed by females. Female kestrels with supplemented nests removed more prey items than control females ($F_{1,41}=102.49$, $P<0.001$), but the number of prey removed decreased between the early and late stages of brood rearing ($F_{1,41}=4.31$, $P=0.04$; Fig. 2). The age by treatment interaction was also significant ($F_{1,41}=4.10$, $P=0.05$). A similar pattern was found for the amount of biomass removed by females with supplemented nests (Fig. 2;

Table 1 Difference (\pm SE) in mean prey delivery rates of female and male American kestrels (*Falco sparverius*) in control and food supplemented nests during the latter part of the brood-rearing period (nestling age 11–24 days old)

Rate	Treatment	Difference between sexes ^a	Paired		
			<i>t</i>	<i>df</i>	<i>P</i>
Prey/h	Control	1.2 \pm 0.3	3.64	37	0.001
	Supplement	0.2 \pm 0.2	1.09	32	0.28
Grams/h	Control	2.5 \pm 0.8	3.05	37	0.004
	Supplement	0.9 \pm 1.0	0.94	32	0.35

^a Differences were calculated by subtracting the average male rates from the average female rates in the same nest. Therefore, positive values represent female-biased prey delivery rates

treatment: $F_{1,41}=85.12$, $P<0.001$; stage of brood rearing: $F_{1,41}=4.58$, $P=0.04$; interaction: $F_{1,41}=4.60$, $P=0.04$). These results suggest that while parent females were removing food (which were predominantly supplements), nestlings had access to at least some of the supplements; the amount of supplements fed increased throughout brood rearing whereas the amount removed by females decreased (Fig. 2). When we analysed the total biomass of prey brought to nests over the course of a day, there were no differences between control and supplemented nests ($F_{1,45}=2.92$, $P=0.10$), although more biomass was delivered during the late stage of brood rearing compared to the early stage ($F_{1,45}=13.55$, $P<0.001$; Fig. 3).

Our results for prey removals appear to indicate that females may have attempted to limit their young's access to supplemental food; however, nestlings may also have received other benefits from food supplementation. After data were ln-transformed to meet assumptions of normality, supplemented females spent more time in nest boxes than control females during both stages of brood rearing (treatment: $F_{1,45}=11.16$, $P=0.002$; stage: $F_{1,45}=267.19$, $P<0.001$; Fig. 4). These latter results suggest that supplementation allowed females more time for brood-

ing, especially when offspring were young, or to prepare food for offspring.

Overall, our results showed that female parents whose nests were provided with supplemental food reduced the number of prey delivered and consequently the biomass delivered to offspring. These benefits may have had fitness consequences, because females whose broods received supplemental food were more likely to return to the study area in subsequent years than control females (Table 2). Male kestrels whose broods received food supplements did not return more often in subsequent years than control males (Table 2). Among birds that returned to the study area, females dispersed farther than males (6.9 ± 7.2 km versus 0.9 ± 1.1 km; $F_{1,21}=4.43$, $P=0.04$), but dispersal distance of birds whose broods were supplemented were not significantly different than control birds (1.3 ± 2.8 km versus $5.5\text{--}6.8$ km; $F_{1,21}=1.53$, $P=0.23$). The sex by treatment interaction also was not significant ($F_{1,21}=0.45$, $P=0.51$).

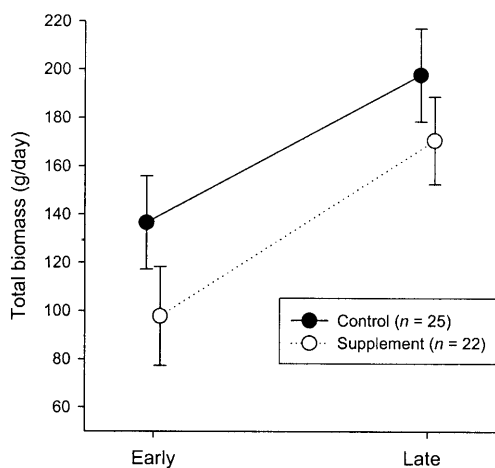


Fig. 3 Average total biomass (\pm SE) of prey received per day by broods of American kestrels at control and food-supplemented nests during early (nestling age 1–10 days old) and late (nestling age 11–24 days old) stages of brood rearing. See Methods for calculation of total biomass

Fig. 4 Average time (\pm SE) spent in nest boxes by control and food-supplemented female American kestrels during **a** early (nestling age 1–10 days old) and **b** late (nestling age 11–24 days old) stages of brood rearing

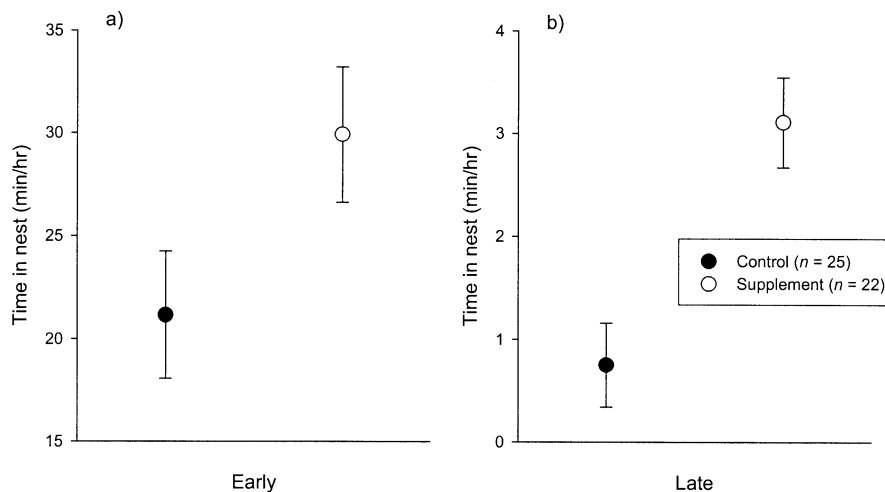


Table 2 Return rate to the study area in subsequent years by adult American kestrels according to whether their nest had received supplemental food or served as a control between 1993 and 1995

Sex	Return rate		<i>G</i>	<i>df</i>	<i>P</i>
	Control	Supplemented			
Female	3/33 (9.1%)	10/31 (32.3%)	5.51	1	0.02
Male	6/17 (35.3%)	6/27 (22.2%)	0.89	1	0.35

Quality and mortality of offspring

Female offspring that received supplemental food were not heavier than controls ($F_{1,58}=1.86$, $P=0.18$), but females were lighter when they experienced inclement weather during brood rearing (covariate, $F_{1,58}=23.56$, $P<0.001$). Similarly, supplemented males fledged at similar weights to males in control nests ($F_{1,56}=0.90$, $P=0.35$), and were significantly lighter when the weather they were exposed to during the nestling period was inclement ($F_{1,56}=25.10$, $P<0.001$). There were no differences in tenth primary length of females between supplemented and control nests ($F_{1,58}=1.66$, $P=0.20$), but primary lengths were shorter when weather was inclement ($F_{1,58}=19.17$, $P<0.001$). For males, there was a significant year by treatment interaction ($F_{2,52}=3.37$, $P=0.04$), so we analyzed years separately. In 1993, males in supplemented nests had longer tenth primaries than those in control nests ($F_{1,10}=10.16$, $P=0.01$), and primary lengths were also significantly affected by weather during brood rearing ($F_{1,10}=6.73$, $P=0.02$). In 1994 and 1995, there were no differences in length of primaries between treatment and control males (1994: $F_{1,13}=0.01$, $P=0.97$, 1995: $F_{1,27}=0.01$, $P=0.91$), nor did variation in weather significantly affect length of tenth primaries of males (1994: $F_{1,13}=3.71$, $P=0.07$; 1995: $F_{1,27}=0.01$, $P=0.99$).

The probability of a nest experiencing mortality was not different between supplemented nests and control nests (logistic regression, $\chi^2=1.10$, $df=1$, $P=0.29$; Fig. 5); however, the probability of mortality in both supplemented and control nests increased as the average day

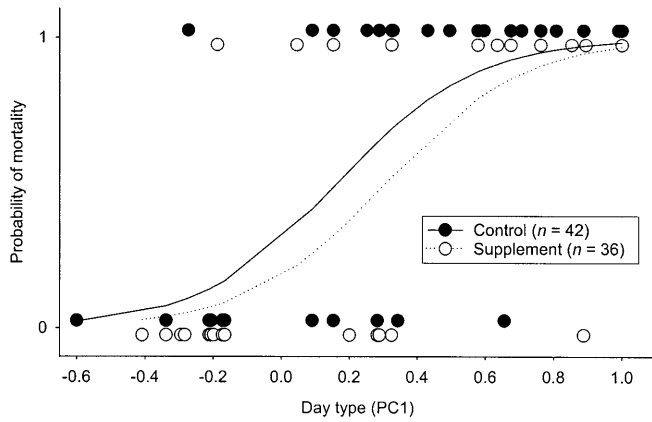


Fig. 5 The probability that nests of American kestrels experience nestling mortality according to the average weather (day type) experienced at the nest over the brood rearing period. Positive values of day type represent inclement weather whereas negative values represent favourable weather. To illustrate the distribution of control and supplemented nests, data points have been offset slightly from 0 and 1

type nestlings were exposed to became more inclement ($\chi^2=23.8$, $df=1$, $P<0.001$; Fig. 5).

Discussion

Parental provisioning rate

American kestrels whose nests received supplemental food brought fewer prey items and less biomass to their nests than control parents (Fig. 1); however, behaviour of each sex of parent was not altered to the same extent. As predicted, female kestrels with supplemented nests responded strongly to our manipulation and significantly reduced both the number of prey and biomass delivered to nests compared to control females (Fig. 1). In contrast to females, the response of male kestrels to extra food was not significant; supplemented males delivered similar numbers and biomass of prey items to nests as controls males (Fig. 1). Overall, provisioning rates of females in control nests were higher than their mates, but when supplemented, females reduced their provisioning rates and there were no differences between the sexes (Table 1). Our results for American kestrels are similar to those previously reported for Eurasian kestrels (*F. tinnunculus*); both hunting effort and prey delivery rates of supplemented females decreased compared to controls, but there were no differences in behaviour of males (Wiehn and Korpimäki 1997).

American kestrels show inherent differences in the role of each sex during brood rearing. Females are largely sedentary during the early nestling period, and males provide most of the food for their mates and brood. Balgooyen (1976, p 33) stated that once female American kestrels begin to hunt for their broods, males no longer transfer prey to females and instead deliver prey directly to the nest. It is possible, even though we limited

our analyses of provisioning to that part of the nestling period where females are hunting, that some of the prey brought by females to nests may actually have been captured by their mates. Furthermore, our supplementation experiment may have also altered the degree to which males transfer prey to their mates. If this occurred, the provisioning rates that we documented in our study may not reflect actual parental effort of each sex because some of the prey delivered by females may actually have been caught by males and subsequently passed to females. If this was the case, we may have overestimated the contributions of females to parental care, and underestimated the contributions of males; therefore, the results that we present may actually be conservative, and the sex-specific strategies much more pronounced than what is shown by our data (Fig. 1). Regardless, several studies of the closely related Eurasian kestrel have shown that prey delivery rates of females are significantly correlated with hunting effort (Tolonen and Korpimäki 1994, 1996), even when supplemental food is provided (Wiehn and Korpimäki 1997). We are therefore confident that the provisioning rates used in our study are a reasonable estimator of parental effort.

Much of the prey brought to nests by females prior to nestlings being 10 days old probably represents prey captured by males that was subsequently transferred to females (Balgooyen 1976; personal observation). The combination of male provisioning and supplemental food may have resulted in there being excess food in the nest, especially early in brood rearing, which allowed females to remove prey, including supplements (see also Wiehn and Korpimäki 1997). Indeed, supplemented females removed prey from nests more often than control females during both the early and late stages of brood rearing (Fig. 2). While some supplemented food was cached and later brought back to nests, females were also observed consuming supplemented mice on numerous occasions. The extra food, reduced work rates, or some combination of both, appeared to have fitness consequences for supplemented females, as they had higher return rates than females in control nests, suggesting higher survival (Table 2). In contrast, we were unable to detect any differences in return rates between supplemented and control males, and although small sample sizes may have limited the power of our test, the patterns in the data were not suggestive (Table 2).

Return rates of parents whose work loads were reduced through supplementation or brood reduction are often higher (Dijkstra et al. 1990; Verhulst 1994; Daan et al. 1996; Korpimäki and Rita 1996; but see Wernham and Bryant 1998). Similarly, parents whose work loads are increased, generally through experimentally enlarged broods, appear to survive less well (Siikimäki et al. 1997). In addition to having survival consequences, increased energy expenditure during parental care may also reduce future fecundity (Gustafsson and Sutherland 1988), even under natural levels of expenditure (Wernham and Bryant 1998). Our results are noteworthy because they demonstrate that even normal levels of en-

ergy expenditure are associated with reproductive costs because when work loads of females were reduced, return rates increased (Table 2).

Return rates are a function of survival, dispersal, and recapture probability (Boulinier et al. 1997). However, we are unable to ascertain whether the cause of higher return rates of supplemented females is due to enhanced survival. We did show that control birds do not disperse farther than supplemented birds, suggesting that differential dispersal cannot account for our results for females. Even if our results are the product of differential dispersal, they may still represent costs because dispersing birds may have difficulty securing a breeding site and mate, and may breed less successfully at the new site (Boulinier et al. 1997; Bensch et al. 1998; Danchin and Cam 2002). Similarly, control females may have returned at similar rates as supplemented females but were not recaptured. We obtained much of our return rate data by capturing kestrels during incubation; our results might therefore indicate that supplemented females were more likely to breed in subsequent years, and so have enhanced future fecundity, compared to control females (see also Danchin and Cam 2002).

Offspring quality and mortality

Although female parents frequently removed food from supplemented nests, and prey delivery rates to supplemented nests were reduced such that average biomass brought per day was not different from control nests (Fig. 3), there was still potential for nestlings to benefit from the experimental addition of food. Female kestrels spent more time in supplemented than control nests during the early stage of the nestling period (Fig. 4), probably brooding young. Parent females also spent more time in supplemented than control nests when nestlings were older (Fig. 4), presumably to facilitate the feeding of young by tearing up prey. Such behaviour may have consequences for food intake rates of offspring, because large vertebrate prey brought to nests may occasionally go uneaten if parents do not open up the carcass (personal observation). Despite these potential advantages associated with supplementation, nestling kestrels receiving extra food were not heavier than controls at fledging. Wiehn and Korpimäki (1997) showed that even though supplemented nestling Eurasian kestrels received on average 10.3 g/day more than offspring in control nests, the extra food did not translate into increased mass at fledging. They speculated that lack of significant differences in mass may result if tissues of supplemented nestlings were more mature, and hence contained less water, than control nestlings.

Our results for length of tenth primary of nestlings at fledging were similar to those for mass. We detected no differences between supplemented and control nestlings, except in 1993 when tenth primaries were longer among male nestlings receiving supplements. Weather in 1993 was very inclement (Dawson and Bortolotti 2000), and it

is possible that significant effects of manipulations are apparent only in particularly bad years (Martin 1987; Boutin 1990; see also below). As we have previously shown (Dawson and Bortolotti 2000), weather experienced during brood rearing had a greater effect on nestling growth than food supply because in nearly all cases, mass and length of tenth primaries at fledging were reduced among nests experiencing inclement weather during brood rearing.

Many food supplementation experiments have shown that extra food reduces offspring mortality in the nest (Korpimäki 1989; Simons and Martin 1990; Richner 1992; Wiehn and Korpimäki 1997), and may also affect postfledging survival and recruitment (Simons and Martin 1990; Verhulst 1994). In contrast, after controlling for the effects of weather, we could find no effect of supplementation on the probability of a nest experiencing mortality (Fig. 5). The fact that mortality occurred even among supplemented nests, and that there were significant effects of weather, suggests that mortality may be the result of acute food shortages, as might occur when relatively short periods of inclement weather prevent parents from foraging effectively for the brood (Dawson and Bortolotti 2000).

Overall, we found few effects of supplementation on offspring quality or mortality. In contrast, Wiebe and Bortolotti (1995a) showed that supplemented broods of American kestrels in our study area had lower mortality and generally were heavier at fledging, despite the fact that parents also reduced their provisioning rates (Wiebe and Bortolotti 1994). Although the studies by Wiebe and Bortolotti also manipulated hatching asynchrony, supplemented broods still performed better than unsupplemented ones regardless of the degree of asynchrony (Wiebe and Bortolotti 1995a). While numerous food manipulation studies have shown that food may have consequences for reproductive success, these effects may only become apparent when abundance of natural food is low (Martin 1987; Boutin 1990). When we compared the average number of small mammals on territories in July during Wiebe and Bortolotti's (1995a) study (13.8 ± 0.9 , $n=148$ territories) to numbers during our study (17.7 ± 0.7 , $n=255$ territories), small mammals were significantly more abundant during our study ($F_{1,401}=12.14$, $P<0.001$). This difference in abundance of natural prey may account for the apparent discrepancy between the present study and that of Wiebe and Bortolotti (1995a). Similarly, Wiehn and Korpimäki (1997) found that supplementation reduced mortality of nestling Eurasian kestrels even during a year of high vole abundance. Although we lack directly comparable data, voles may have been less abundant in Wiehn and Korpimäki's (1997) study than in ours.

Sex-specific provisioning strategies

Theory suggests that as provisioning rates increase, offspring survival should also increase, but with diminish-

ing returns; concurrently, costs of provisioning increase at an accelerating rate (Winkler 1987). When resources become abundant, such as occurred when supplemental food was provided, females reduced their level of provisioning, and as a result had higher return rates. Male kestrels with supplemented nests delivered similar number and biomass compared to control males (Fig. 1); they did not react as strongly to supplementation as did their mates. This less flexible behaviour of males in response to abundant resources may be suboptimal. Because their own survival was not enhanced, and offspring quality or mortality in supplemented nests were similar to that in control nests, supplementation appeared to have had little fitness advantages for males.

The lack of an identical response to supplemental food by each sex may be the result of differing roles of each sex during breeding. Male kestrels almost never enter the nest during brood rearing, whereas females spend considerable time in (Fig. 4) and near the nest (Balgooyen 1976; personal observation). Thus, females may be more aware of the nutritional needs of their offspring than are males. A similar explanation has been proposed for the lack of response to supplemental food by Eurasian kestrels (Wiehn and Korpimäki 1997). Alternatively, the less flexible strategies of male American kestrels may be beneficial. It has been shown that parent birds lose mass throughout the reproductive event, and this appears more common in females than males (Martin 1987). Food supplementation often reduces or eliminates mass loss by females (Garcia et al. 1993; Wiehn and Korpimäki 1997). In addition, supplemented females are better able to initiate second clutches, or replacement clutches if their first clutch fails (Arcese and Smith 1988; Simons and Martin 1990), presumably because they are in better condition. Male kestrels may be at an advantage if their mates are relatively sedentary and in better condition, and so better able to initiate a second clutch if the first clutch fails or is lost to predators. Although the consideration of raising two broods in a season may also be important for some species, it would be of little consequence for kestrels in our study area, which only raise a single brood in a season (personal observation). Predators may also shape the division of labour between the sexes, as the presence of the female at the nest is thought to reduce predation (Newton 1979); however, we have no conclusive evidence that any of the nests lost during the brood-rearing period in our study were the results of predators.

Conclusions

Our experiment showed that food supply had consequences both for the behaviour and fitness of parent American kestrels. Because supplementation caused parents to reduce their provisioning, offspring did not benefit from extra food. This suggests that parents were more sensitive to potential costs of reproduction as opposed to any benefits that may have accrued through increased

offspring quality or survival. In addition, food supply appears to have greater consequences for females than males because females reduced their work rates more and as a result had higher return rates. The amount of food that we provided was enough to approximately meet the energy requirements of a single nestling. Compared to other studies (e.g., Wiehn and Korpimäki 1997; Dewey and Kennedy 2001), our feeding regime was relatively modest. Moreover, given that abundance of natural food during our study was relatively high, these results, coupled with results from previous investigations on our study population (Bortolotti et al. 1991; Wiebe and Bortolotti 1992, 1994, 1995a, b; Dawson and Bortolotti 2000), affirm that food supply is an important determinant of parental behaviour and reproductive success of kestrels.

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