

# Parental effort of American kestrels: the role of variation in brood size

Russell D. Dawson and Gary R. Bortolotti

**Abstract:** Brood size has the potential to determine the allocation of resources between parents and offspring, as well as influence the relative contributions of each sex to parental effort. However, it is unclear whether brood size is the proximate determinant of parental effort, or conversely whether parental effort is the proximate factor to which brood size is adjusted. If brood size determines parental effort, then theory suggests that parental effort should vary with experimental changes in brood size. In contrast, if parental effort determines brood size, then parental effort is expected to be independent of experimental variation in brood size. To distinguish between these hypotheses, we experimentally reduced brood sizes of American kestrels (*Falco sparverius*). Our results suggest that male parents responded to brood-size variation and adjusted their provisioning behaviour accordingly. Conversely, female parents did not adjust provisioning in response to brood size, and as a result, offspring in reduced broods received more food on a per-nestling basis. However, condition and survival of offspring were similar in reduced broods and control young, which may have been the result of larger food requirements of small broods, owing to increased thermoregulatory costs compared with control broods. Female parents with reduced broods also did not brood offspring more often, further suggesting that females do not respond to variation in brood size. We conclude that the proximate determinants of parental effort are sex-specific in American kestrels: for males, brood size determines behaviour, whereas for females, behaviour may be a proximate factor determining brood size.

**Résumé :** La taille de la couvée peut potentiellement déterminer l'allocation des ressources entre les parents et les rejets et influencer les contributions relatives de chacun des sexes à l'investissement parental. Il n'est cependant pas clair si la taille de la couvée est le facteur déterminant immédiat de l'investissement parental ou si, à l'inverse, l'investissement parental est le facteur immédiat auquel la taille de la couvée s'ajuste. Si c'est la taille de la couvée qui détermine l'investissement parental, la théorie écologique prédit que l'investissement parental devrait varier avec les changements expérimentaux de la taille de la couvée. Au contraire, si c'est l'investissement parental qui détermine la taille de la couvée, il devrait être indépendant de toute variation expérimentale de la taille de la couvée. Pour choisir entre ces hypothèses, nous avons réduit de manière expérimentale la taille des couvées de crécerelles d'Amérique (*Falco sparverius*). Nos résultats laissent croire que les parents mâles réagissent à la variation de la taille de la couvée et ajustent leur comportement d'approvisionnement en conséquence. En revanche, les parents femelles n'ajustent pas leur approvisionnement en fonction de la taille de la couvée et, en conséquence, les oisillons des couvées plus petites reçoivent plus de nourriture par oisillon. Cependant, la condition et la survie des oisillons des couvées restreintes sont semblables à ceux des oisillons des couvées témoins, ce qui peut refléter les besoins plus élevés de nourriture chez les petites couvées, à cause des coûts plus importants de la thermorégulation chez les petites couvées que chez les couvées témoins. Les parents femelles des couvées moins nombreuses ne produisent pas non plus d'oisillons plus fréquemment, ce qui est une preuve de plus qu'elles ne réagissent pas à la variation de la taille de la couvée. Nous concluons donc que les facteurs déterminants immédiats de l'investissement parental sont reliés au sexe chez la crécerelle d'Amérique; la taille de la couvée détermine le comportement des mâles, alors que, chez les femelles, le comportement peut être un facteur déterminant immédiat de la taille de la couvée.

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## Introduction

Provisioning offspring is an energetically expensive activity for parent birds raising altricial young (Drent and Daan 1980; Masman et al. 1988). Such energy expenditures are potentially costly because they may decrease parental sur-

vival, reduce future fecundity, or both (Williams 1966; Roff 1992; Stearns 1992). As a result, parents are expected to balance the costs and benefits of reproduction so that fitness is maximized (Williams 1966). The nestling period is therefore a critical time for behavioural decisions by parents regarding how much effort they should invest in current reproduction (Martins and Wright 1993).

Natural selection is expected to favour parents that optimize their reproductive value at each breeding episode (Winkler 1987). Because the reproductive value of a parent is the sum of current reproductive output and future reproduction, it is predicted that selection will favour individuals that adjust their parental effort in relation to the fitness costs and benefits of the current brood (Winkler 1987). One possible mechanism on which to base their parental-effort decisions is the value of the current brood, either quality or quantity of off-

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spring (Curio et al. 1984; Montgomerie and Weatherhead 1988). For example, Nur's (1984) model of parental care predicts that if parents maximize the difference between costs and benefits of feeding offspring, increases in brood size will generally be accompanied by increases in feeding rates (see also Winkler 1987). The ability to respond to current offspring has been termed a flexible investment strategy (Johnsen et al. 1994).

Alternatively, Morris (1985, 1987) hypothesized that parental decisions regarding total investment in a reproductive event are based primarily on the cost-benefit analysis of parental survival as a function of that investment, rather than on proximate indicators such as current brood size. Therefore, brood size is the result of optimal allocation of investment among offspring rather than the cause of such investment decisions (Morris 1987). When faced with surplus resources, such as occurs when brood size is reduced, parents can either allocate all the surplus to offspring, or they may withhold it and enhance their future reproduction. Morris (1987) predicted that allocation of extra resources to offspring would be more likely to occur, because parental investment should be independent of brood size. Morris' (1987) hypothesis is functionally similar to the "fixed-level hypothesis" of Johnsen et al. (1994): parental investment decisions are fixed and insensitive to the current needs of the offspring (e.g., Ricklefs 1992).

In this paper we test whether parental effort of the American kestrel (*Falco sparverius*), a small falcon, is the proximate determinant of brood size (fixed investment strategy), or conversely whether brood size determines parental effort (flexible investment strategy). The fixed investment strategy predicts that there will be no effect of manipulated brood size on parental effort and, as a result, manipulations of brood size will result in a trade-off between offspring quality and number (Morris 1987). The flexible investment strategy predicts that parents respond to the needs of their brood and so will adjust their parental effort according to brood size (Winkler 1987); because parents meet the energetic demands of their offspring, quality of offspring will be independent of brood size. The specific aims of this investigation were to document whether decisions regarding parental effort, measured as food provisioning to the nest, (i) varied with experimental brood size, (ii) varied between the sexes, and (iii) whether such decisions had fitness consequences for parents (survival rates estimated from return rates) or offspring (condition and mortality while in the nest).

Researchers investigating clutch-size variation have often increased the number of young that parents had to raise (reviews in Lindén and Møller 1989; Dijkstra et al. 1990; Golet et al. 1998). However, Winkler (1987) has shown that while parental effort may increase with brood size (Nur 1984), such increases in effort may not be observed if parental effort is constrained. Parents may employ a flexible investment strategy, but are simply incapable of responding to brood enlargements if such manipulations result in the upper limits of parental work rates being exceeded (Drent and Daan 1980). It is not possible, therefore, for brood enlargements to adequately test whether investment strategies are fixed or flexible, because if no response in behaviour of parents is seen, one cannot distinguish between these two hypotheses. A lack of response may be due to levels of parental effort being

fixed and inflexible; however, it is also plausible that parents are employing a flexible investment strategy but are unable to respond to the manipulation because they simply cannot increase their work rates. Therefore, in this study we reduced brood sizes of kestrels by one nestling and compared these nests with unmanipulated control nests.

Given that previous investigations on our study population have shown that parent American kestrels facultatively manipulate many aspects of their reproductive behaviour (e.g., Wiebe and Bortolotti 1992, 1994), we predicted that kestrels would employ a flexible investment strategy and significantly reduce their parental effort in response to reductions in brood size. Moreover, we predicted that female kestrels would show a stronger response to our manipulation than would males, especially given the distinct role of each sex in raising young. Males provide most of the food for the female and the brood until the young are about 10 days of age (Balgooyen 1976; personal observation). Typically, males transfer prey to their mates in the vicinity of the nest, while females feed and brood the young as well as guard the nest (Balgooyen 1976; personal observation). Because females spend more time at nests, particularly during the early stages of brood rearing, they should be more aware of the nutritional needs of their offspring and so more likely to adjust their behaviour in response to variation in brood size.

## Materials and methods

We studied a wild population of American kestrels from 1993 to 1995 in the boreal forest near Besnard Lake, Saskatchewan, Canada (55°N, 106°W). Approximately 370 nest boxes were placed in a variety of habitats along an extensive network of roads and logging trails (approximately 300 km), and 150–200 pairs bred in them annually (Bortolotti 1994). Kestrels arrived on territories in mid to late April and began to lay eggs in mid-May. For this study, we used only nests that had 5 eggs, the most common clutch size in our population. Very few pairs have larger clutches (1.2%; Tella et al. 2000). Nests were randomly assigned to either a treatment or a control group. Within 1 or 2 days after hatching, we removed a single nestling from treatment nests to reduce brood size to 4 nestlings, and placed these young in other nests that were not part of this study. We always removed nestlings that hatched mid-sequence so as not to alter the size hierarchies between the largest and smallest offspring within a nest. We compared reduced nests with the sample of control nests that had 5 nestlings. In several cases, hatching failure resulted in fewer than 5 young being present in a nest after hatching was completed. In these cases, we added foster young from other nests not used in this study to maintain a brood size of 5 nestlings in control nests and 4 nestlings in reduced nests. In total, brood size was reduced at 38 nests ( $n = 14$  in 1993;  $n = 9$  in 1994;  $n = 15$  in 1995), while another 38 nests served as controls ( $n = 13$  in 1993;  $n = 9$  in 1994;  $n = 16$  in 1995). Our protocol was approved by the University of Saskatchewan Animal Care Committee on behalf of the Canadian Council on Animal Care.

Parental effort was estimated using provisioning rates to nests. We placed video cameras approximately 5–15 m from nest boxes and taped all visits to the nest by adults. Nestling age ranged from 11 to 25 days during observation periods

(see below). Observations were made at random times between 0700 and 2000, and although each period was at least 2 h, nearly all were the length of the videotape ( $2.70 \pm 0.002$  h (mean  $\pm$  SE),  $n = 198$  observation periods). Each nest was observed at least once, and most were observed on several days ( $7.05 \pm 0.43$  h,  $n = 76$  nests). From each tape, we counted the trips per hour 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 order. By measuring the length of each prey item on the video monitor with digital callipers, as well as at least two dimensions of the nest boxes as they appeared on the video monitor, we were able to estimate the actual size of the prey items that were delivered. Using length–mass relationships derived from a sample of representative prey captured with snap traps (mammals; see Dawson and Bortolotti 2000) or sweep nets (invertebrates) or by measuring prey in nest boxes (birds and amphibians), we were able to calculate the biomass of each prey item. Although kestrels feed on a wide variety of prey (Bortolotti et al. 2000), the number of prey brought to nests is correlated with biomass ( $r = 0.65$ ,  $n = 76$  nests,  $P < 0.001$ ). In this paper, we present results only from analyses using number of prey because results for biomass were qualitatively similar.

In addition to quantifying provisioning, we also documented the amount of time parents spent in the nest box when chicks were between 1 and 10 days old, as well as the amount of prey removed by parents during this time. These data were obtained in the same manner as those for provisioning. Observations were made at 31 control and 36 reduced nests, and each nest was observed for  $3.70 \pm 0.23$  h (mean  $\pm$  SE;  $n = 67$  nests). It is very rare for male parents to brood offspring, and males generally do not remove prey from nests (Dawson and Bortolotti 2002), so these data were analyzed for female parents only.

We trapped adult kestrels throughout our study using bal-chatri traps during the prelaying period (Berger and Mueller 1959) and in the nest box by hand during incubation. Each bird was banded with a unique combination of aluminum and coloured plastic leg bands. We determined return rates of adults by recapturing kestrels on the study area from 1994 to 1997. Using hand-held global positioning systems, we also measured the distance between the original nest of each returning bird and its nest upon returning to the study area in subsequent years.

To test for effects of brood-size manipulations on quality of nestling kestrels at fledging, we measured body mass (to the nearest gram) and length of the tenth primary feather (to the nearest millimetre) when nestlings were 24 days old, just prior to fledging. During routine visits to nests throughout brood rearing, we also documented whether mortality had occurred since the last visit, and when possible we attempted to maintain a brood size of 5 nestlings in control nests and 4 nestlings in reduced nests by replacing dead nestlings with those from other nests that were not part of this study. When replacement nestlings were unavailable, the nest was excluded from further study.

### Statistical analysis

To test whether kestrels employed fixed or flexible investment strategies, we analyzed provisioning data from the pe-

riod when offspring were between 11 and 25 days old. We limited our analyses to this age period because prior to it, data may be 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 majority of prey are actually captured by the male parent (Balgooyen 1976; personal observation). Once offspring are older than 10 days, female parents begin to hunt to provision their broods. Balgooyen (1976:33) stated that once female American kestrels begin to hunt to provision their broods, males no longer transfer prey to females and instead deliver them directly to the nest. Limiting our analyses to the period when nestlings were over 10 days of age allowed us to be more confident that the patterns of prey deliveries accurately reflected the contributions of each sex to parental care.

To determine how brood size affected decisions regarding parental effort, we analyzed the rate of prey deliveries to the nest (i.e., number of prey/h per nest). However, the growth and well-being of an individual nestling, and therefore its parents' fitness, also depend upon what portion of that food it receives on average. Therefore, given that one goal of this study was to investigate whether parental decisions had fitness consequences for offspring, we also investigated provisioning on a per-nestling basis, using number of prey per nestling (number of prey/h per chick). For both of these analyses, we used repeated-measures analysis of variance (ANOVA) with brood size and year as the between-subjects factors, sex of the parent as the within-subjects factor, and nestling age as a covariate. A repeated-measures design was used because we were interested in determining not only how brood size affected overall provisioning on a per-nest or per-chick basis, but also how each member of the pair responded to our manipulation; if there were sex differences in the response to variation in brood size, then a significant sex-by-treatment interaction would be expected (e.g., Dawson and Bortolotti 2002). To test for differences between brood sizes in the amount of time spent in nest boxes by females when the young were 10 days of age or less, analysis of covariance (ANCOVA) with nestling age as a covariate was used. For all of the above analyses, terms (except for the explanatory variable of interest, brood size) and interactions were iteratively removed from models if significance was not approached ( $P > 0.10$ ), and analyses were repeated. A Mann–Whitney  $U$  test was used to test for effects of brood size on biomass of prey removed by females when young were between 1 and 10 days old. When more than one observation from an individual nest appeared in any of the above datasets, the mean value for that nest was used in analyses.

To test for effects of brood-size manipulation on survival of adult kestrels, we used return rates as a surrogate for survival. For each sex, we first tested for heterogeneity in return rates among years (see Zar 1999), and finding none ( $P > 0.05$ ) we pooled data from all 3 years to increase statistical power.  $G$  tests were then used to determine whether return rates of each sex of parent varied among brood sizes. We also tested whether brood-size manipulation affected the dispersal distances of returning parents, using ANOVA with sex and treatment as explanatory variables.

Kestrels are sexually dimorphic in size as nestlings (Dawson and Bortolotti 1999), so to test for effects of brood-size ma-

nipulations on quality of offspring, we calculated means for mass and length of the tenth primary of males and females separately for each nest. To avoid any nest appearing more than once in analyses, we analyzed data for each sex separately rather than using sex as a factor. Because the weather experienced over the brood-rearing period had significant effects on offspring quality (Dawson and Bortolotti 2000, 2002), we included a weather variable as a covariate in analyses. Using mean daily temperature ( $^{\circ}\text{C}$ ), wind speed (m/s), and total amount (mm) and duration (h) of precipitation as input variables, we performed a principal-components analysis. The first principal component (PC1) from this analysis is a continuous variable where at the extremes, positive values represent cool, windy days with rainfall lasting many hours, while negative values represent warm, calm days without precipitation. For each nest, PC1 values were averaged over the brood-rearing period (from 1 day after hatching to 23 days of age, just prior to fledging) to produce a variable, "day type", that described average weather conditions experienced by a nest (details in Dawson and Bortolotti 2000). We then used ANCOVA with treatment as the explanatory variable of interest, and day type as a covariate. We iteratively removed nonsignificant terms and interactions, and always keeping treatment in the model, repeated analyses.

As with nestling condition, mortality of nestlings was significantly affected by weather during brood rearing (Dawson and Bortolotti 2000, 2002). To test whether control nests and those with reduced brood size differed in their probability of having at least one nestling die before 24 days of age, we used a logistic regression model with mortality (yes/no) as the binary dependent variable, brood size as a categorical variable, and day type as a covariate.

Statistical analyses were performed using SPSS (Norusi 1993) and SAS (SAS Institute Inc. 1990). All tests are two-tailed and means are presented  $\pm 1$  SE.

## Results

### Parental behaviour and return rates

Our repeated-measures ANOVA showed that there was no significant difference between control nests and those with reduced brood size in the total number of prey brought to the nest by parent kestrels ( $F_{[1,74]} = 0.30$ ,  $P = 0.58$ ; Fig. 1). This analysis also showed that females brought more prey than did their mates ( $F_{[1,74]} = 30.17$ ,  $P < 0.001$ ), and there was some suggestion of a sex-by-treatment interaction ( $F_{[1,74]} = 3.00$ ,  $P = 0.08$ ). This interaction, though not significant, was the consequence of females with control nests bringing slightly fewer prey than females with reduced nests, while rates of delivery by control males were slightly higher than those by males with reduced nests. The effects of our manipulation are best illustrated by comparing prey-delivery rates between the sexes within nests: females with control nests brought  $1.2 \pm 0.3$  prey items per hour more than their mates, whereas females with reduced broods brought  $2.4 \pm 0.6$  more prey per hour than their mates.

When data were analyzed on a per-nestling basis, parents brought significantly more prey items ( $F_{[1,74]} = 3.95$ ,  $P = 0.05$ ) to reduced nests than to control nests (Fig. 1). These analyses showed that differences in provisioning were largely driven by the behaviour of females, who brought sig-

nificantly more prey items per nestling than did their mates ( $F_{[1,74]} = 28.95$ ,  $P < 0.001$ ). The sex-by-treatment interaction was also significant ( $F_{[1,74]} = 4.87$ ,  $P = 0.03$ ), suggesting that reducing brood size had different effects on the provisioning behaviour of each sex of parent. In contrast to our predictions, these results collectively suggest that females were not adjusting prey deliveries in response to the number of young in their nests, whereas because similar numbers of prey were delivered per nestling by males regardless of brood size, males were responding to reductions in brood size. Age of nestlings was not a significant factor in any of the above analyses.

The results for per-nestling provisioning show clearly that male parents reduce their provisioning in response to a decrease in brood size, whereas female do not. In contrast, this pattern is not readily apparent in the analyses of provisioning on a per-nest basis (Fig. 1), unless one compares the relative contributions of the sexes within a nest (see above). If males are indeed adjusting provisioning in response to the number of young in their nests, our relatively weak manipulation of removing only a single nestling from the brood may not have been sufficient to reveal differences in provisioning at the level of the brood. Stronger effects of reducing brood size may have been seen in analyses of provisioning on a per-nest basis if brood size had been reduced by more than a single nestling.

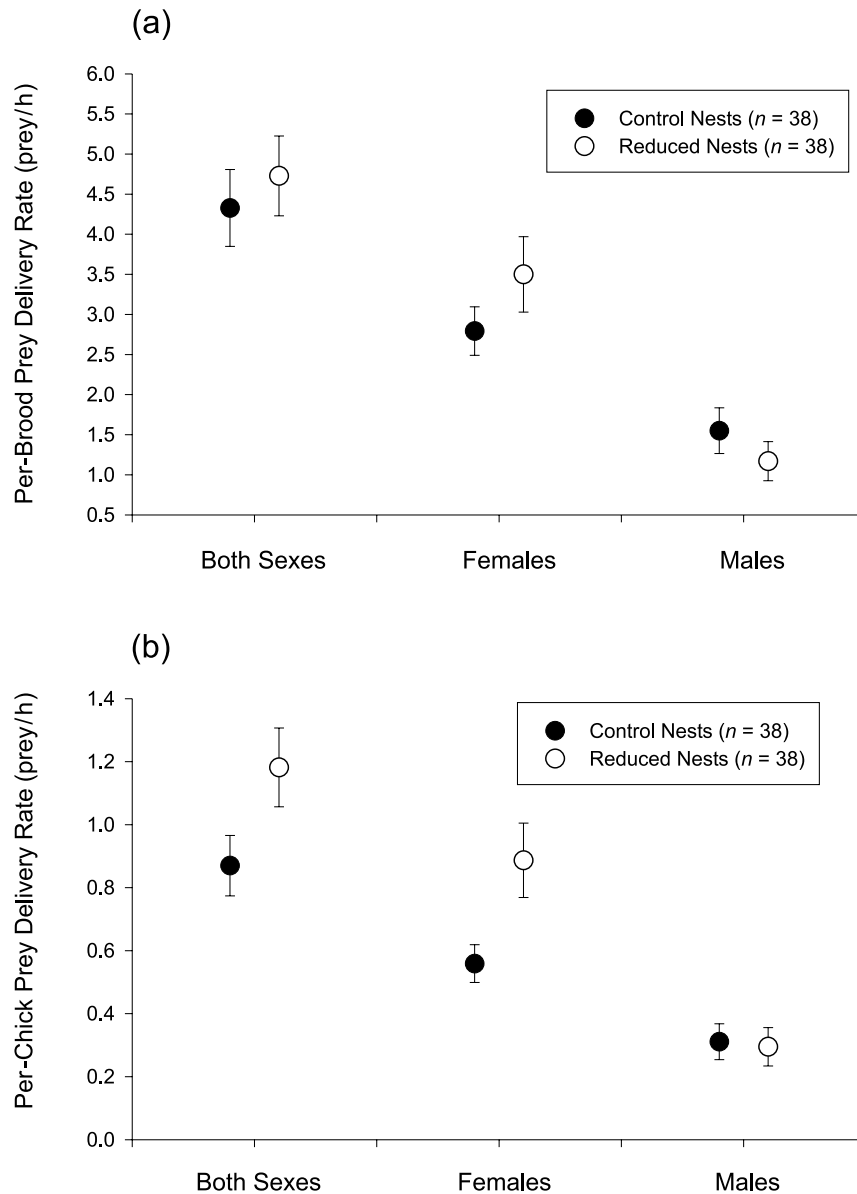
The amount of time that female kestrels spent in nest boxes when young were between 1 and 10 days of age varied annually ( $F_{[2,62]} = 5.86$ ,  $P < 0.01$ ), and decreased as nestlings became older (age covariate:  $F_{[1,62]} = 40.41$ ,  $P < 0.0001$ ); however, we could not detect a difference between reduced ( $25.7 \pm 2.1$  min/h) and control nests ( $22.3 \pm 2.3$  min/h;  $F_{[1,62]} = 1.15$ ,  $P = 0.28$ ). Prey removal by female parents with control broods occurred at only 1 of 31 nests observed, whereas we documented prey removal at 8 of 36 reduced nests (Fisher's exact test,  $P = 0.031$ ). As a consequence, significantly more biomass was removed by females with reduced broods ( $0.47 \pm 0.15$  g/h) than by those with control broods ( $0.01 \pm 0.16$  g/h;  $U = 944$ ,  $P = 0.02$ ).

Seven of 35 (20%) female parents with reduced nests returned to the study area in years after their nests were manipulated. Fewer control females returned (4/38, or 10.5%), but these differences were not significant ( $G = 1.29$ ,  $df = 1$ ,  $P = 0.26$ ). The numbers of males returning were also similar regardless of whether they raised broods with reduced size (9/29, or 31.1%) or had control broods (10/22, or 45.5%;  $G = 1.11$ ,  $df = 1$ ,  $P = 0.29$ ). Among adult birds that returned to the study area, there was no effect of brood size on dispersal distance (reduced broods:  $1.02 \pm 0.46$  km; control broods:  $1.41 \pm 0.51$  km;  $F_{[1,27]} = 0.33$ ,  $P = 0.57$ ), although females dispersed farther than males ( $2.06 \pm 0.56$  versus  $0.38 \pm 0.42$  km;  $F_{[1,27]} = 5.82$ ,  $P = 0.02$ ). These results show that there was no differential dispersal due to our brood-size manipulation and so our estimates of return rates are unlikely to be biased (see Daan et al. 1996).

### Offspring quality and mortality

Female nestlings from reduced broods were not heavier than controls at fledging ( $F_{[1,57]} = 0.33$ ,  $P = 0.57$ ; Table 1), but females were heavier when they had experienced favourable weather during the brood-rearing period (covariate,  $F_{[1,57]} =$

**Fig. 1.** Number of prey items (mean  $\pm$  SE) brought in total (a) and per nestling (b) by parent American kestrels (*Falco sparverius*) to control nests (5 young) and nests where the brood size was reduced (4 young) when nestlings were between 11 and 25 days of age. Categories represent provisioning by the sexes combined and each sex separately.



**Table 1.** Body mass and length of tenth primaries of nestling American kestrels (*Falco sparverius*) at 24 days of age (minimum fledging age) in 5-chick control nests and nests where brood size was reduced to 4 young.

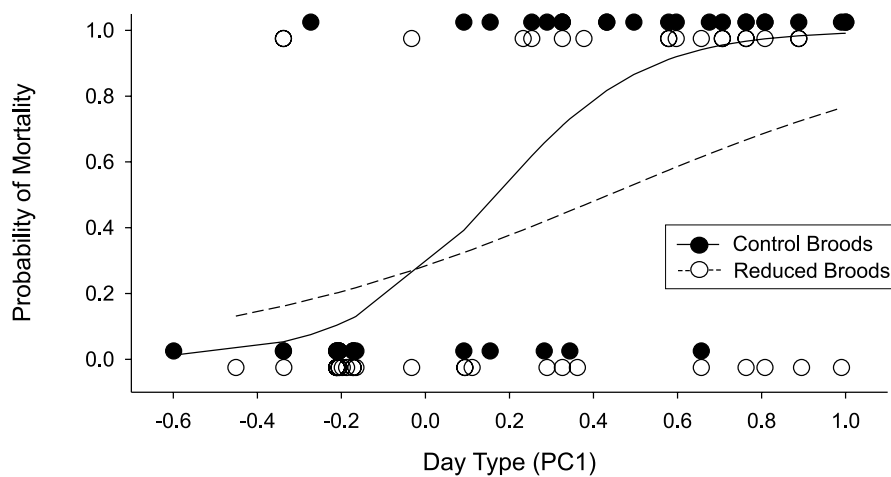
	Body mass (g)		Length of tenth primary (mm)	
	Control brood	Reduced brood	Control brood	Reduced brood
Females	122.8 $\pm$ 1.6 (n = 31)	124.1 $\pm$ 1.7 (n = 29)	61.1 $\pm$ 1.1 (n = 31)	60.4 $\pm$ 1.2 (n = 29)
Males	113.1 $\pm$ 1.4 (n = 30)	115.2 $\pm$ 1.8 (n = 32)	59.1 $\pm$ 1.2 (n = 30)	59.8 $\pm$ 1.1 (n = 32)

**Note:** Sample sizes refer to the number of nests. Except for mass of males, least-square means (PROC GLM; SAS Institute Inc. 1990) are presented, owing to significant effects of weather experienced by nestlings on mass and length of tenth primary at fledging.

15.21,  $P < 0.001$ ). Male nestlings in reduced broods also fledged at similar mass to control males ( $F_{[1,59]} = 0.91$ ,  $P = 0.34$ ; Table 1); however, unlike that of females, mass of males was not significantly affected by weather (covariate,  $F_{[1,59]} = 1.27$ ,  $P = 0.26$ ). Experimental brood-size manipula-

tion also had no effect on the length of the tenth primary (Table 1) of either female ( $F_{[1,57]} = 0.21$ ,  $P = 0.65$ ) or male ( $F_{[1,59]} = 0.18$ ,  $P = 0.68$ ) nestlings at fledging, but primaries of both sexes were longer when the average day type experienced during the brood-rearing period was favourable

**Fig. 2.** Results from a logistic regression for the probability that nests of American kestrels experience offspring mortality according to the average weather (day type) experienced at the nest over the brood-rearing period ( $P < 0.01$ ). Positive values for day type represent inclement weather, while negative values indicate favourable weather. Mortality is defined as either 0 (no nestlings within a nest dying) or 1 (at least one nestling dying). To illustrate the distribution of control nests (5 nestlings) and nests with reduced brood size (4 nestlings), data points have been slightly offset from 0 and 1.



(covariate, females:  $F_{[1,57]} = 19.94$ ,  $P < 0.0001$ ; males:  $F_{[1,57]} = 31.56$ ,  $P < 0.0001$ ).

The probability of a nest experiencing mortality did not differ between reduced and control nests (logistic regression,  $\chi^2 = 0.01$ ,  $df = 1$ ,  $P = 0.97$ ); however, the probability of mortality increased as the average day type to which nestlings were exposed became more inclement ( $\chi^2 = 6.74$ ,  $df = 1$ ,  $P < 0.01$ ; Fig. 2). The brood size by day type interaction was also significant ( $\chi^2 = 3.93$ ,  $df = 1$ ,  $P = 0.05$ ), suggesting that effects of day type appeared slightly earlier and were more pronounced among control nests than among reduced nests (Fig. 2).

## Discussion

### Relationship between brood size and provisioning by parents

Parent American kestrels delivered similar total amounts of food to nests where brood size was experimentally reduced as they did to control nests. As a consequence, significantly more prey were delivered per nestling to reduced nests than to control nests (Fig. 1), suggesting that overall feeding rates of parents were not adjusted in response to the number of young present. Because overall provisioning was unaffected by variation in brood size (Morris 1987), our results appear to support the idea that provisioning rates are fixed in kestrels. Results from a previous study in Quebec also suggested that American kestrels do not appear to alter provisioning in response to experimentally altered brood size (Gard and Bird 1990). However, Gard and Bird (1990) performed behavioural observations throughout the nestling period, but apparently did not control for age effects in their analyses.

When we used repeated-measures analyses to explore the role of brood-size variation in provisioning for each sex of parent separately, we found that per-nestling provisioning rates were higher for reduced broods than for control broods, and that females provisioned more than their mates (Fig. 1). Interactions between brood size and sex in these analyses, as

well as analyses performed on overall provisioning rates, also suggested that there are differences between the sexes in how they respond to changes in brood size: males appeared to respond to reductions in brood size, whereas females did not. Taken together, these results suggest that males may use brood size to adjust their provisioning rates, but that females apparently do not use brood size as a proximate factor upon which to base decisions regarding parental effort.

That female kestrels did not respond to brood-size variation may also be a consequence of constraints on provisioning. It may be that provisioning rates of females with broods of 4 nestlings represent their maximum work rates; females with broods of 5 should be provisioning at a higher rate but are simply unable to do so (Winkler 1987). If females were constrained in this manner, then a response to our brood-size manipulation might not have been expected. However, other data from our study population suggest that this is not the case. We have previously shown that female kestrels raising broods of 5 young respond strongly to the addition of extra food at the nest and decrease their provisioning rates significantly (Dawson and Bortolotti 2002). If provisioning by females raising 5 young was constrained, then we would not have seen such a marked reduction in their provisioning when we provided them with extra food.

Studies on Eurasian kestrels (*Falco tinnunculus*) have shown that parents do not respond strongly to short-term manipulations of brood size (Tolonen and Korpimäki 1996), nor do male Eurasian kestrels increase their hunting effort in response to natural variation in brood size (Masman et al. 1989; Dijkstra et al. 1990; Tolonen and Korpimäki 1994). These results also suggest that parental effort is set to a level where parental survival is not jeopardized, and that brood size is adjusted accordingly (Morris 1985, 1987; see also Wiehn and Korpimäki 1997). However, in contrast to the above studies, Dijkstra et al. (1990) and Deerenberg et al. (1995) showed that hunting effort of both sexes of Eurasian kestrels increased with brood size when number of young was manipulated, suggesting that parental-investment decisions were flexible and proximally determined by brood size. Like-

wise, numerous studies have shown that prey-delivery rates or daily energy expenditures of parents were positively correlated with manipulated brood size in a variety of species (e.g., Nur 1984; Martins and Wright 1993; Sanz 1997; Verhulst and Tinbergen 1997; Wright et al. 1998). The results of these studies, as well as our own, suggest that proximate determinants of parental investment may differ among species, within species in different areas, and also between the sexes.

### Effects of provisioning on offspring

Fledging mass of passerine birds is often positively correlated with postfledging survival (Merilä and Wiggins 1995) and even competitiveness as adults (de Kogel 1997). Despite the fact that nestling kestrels in reduced broods received more prey on a per-nestling basis (Fig. 1), they did not fledge with greater body mass or with longer tenth primaries than control nestlings (Table 1); however, fledging mass of females and length of tenth primaries of both sexes were significantly affected by the weather to which they were exposed during the brood-rearing period (see also Dawson and Bortolotti 2000, 2002). Similarly, there was no effect of brood size on the probability of a nest experiencing mortality, although weather also contributed significantly to nestling mortality (Fig. 2).

The lack of significant differences in quality or mortality of nestlings from broods of different sizes regardless of whether or not more food was available to them may have resulted from differences in energy expenditure of nestlings between brood sizes. Royama (1966) found that smaller broods of great tits (*Parus major*) did not grow faster despite receiving more food per nestling than larger broods, and he suggested that because smaller broods have a relatively larger surface area to volume ratio, they require more food to maintain homeothermy. Subsequent metabolic (O'Connor 1975; Bryant and Gardiner 1979; Clark 1984) and behavioural (Johnson and Best 1982) studies have provided support for Royama's ideas. In this study, female kestrels with reduced nests did not spend more time in nest boxes than control females when the young were between 1 and 10 days of age. Because thermoregulatory costs may have been higher for reduced broods, nestlings may have used the additional food that they received (Fig. 1) to offset these higher costs as opposed to increasing their body mass or feather growth (Table 1).

### Are there costs of reproduction?

According to Morris' (1985, 1987) hypothesis that parents employ a fixed investment strategy, parental effort is insensitive to proximate investment indicators like brood size. While reproduction should not occur without risk, and therefore there would be some basic level of costs (breeders would incur costs that non-breeders would not; e.g., Golet et al. 1998), there should be no apparent cost of reproduction as a function of brood size (Morris 1987). In agreement with this, female kestrels with reduced broods did not adjust their reproductive effort in response to brood size, and had return rates statistically similar to those of control females.

If parents adjust their effort according to brood size, then costs are expected to decline as the number of offspring raised is experimentally reduced (see Nur 1984; Winkler 1987). While there was evidence that male kestrels adjusted

their provisioning strategies according to brood size, there were no detectable differences in return rates between brood sizes. Moreover, the direction of the relationship was opposite to that predicted. The potential advantages gained by reducing broods by one nestling may not have been sufficient to cause differences in return rates. For example, a food-supplementation study on American kestrels showed large effects on female parents, reducing their work rates as well as providing them with extra food (Dawson and Bortolotti 2002). Even with food supplementation, the effect on return rates of females was not dramatic, so the relatively weak effects of our brood-size manipulation (Fig. 1) may explain the lack of differences in survival between brood sizes. A previous study on Eurasian kestrels was also unable to demonstrate effects of manipulated brood size on parental return rates (Korpimäki and Rita 1996; but see Dijkstra et al. 1990; Daan et al. 1996; Deerenberg et al. 1995). As large sample sizes are necessary to detect costs of reproduction (Graves 1991), the sample sizes in our study may have been insufficient to demonstrate such effects.

### Conclusions

Previous research has shown that male and female parents often respond similarly to brood-size manipulations (e.g., Dijkstra et al. 1990; Sanz 1997; Verhulst and Tinbergen 1997; Wright et al. 1998; but see Moreno et al. 1995). In contrast, we detected sex-specific responses in this study: males adjusted their feeding rates in response to brood size more closely than did females (Fig. 1). Despite receiving more food on a per-nestling basis, chicks in reduced broods fledged in similar condition and had similar survival probabilities to control nestlings. We suggest that more food may be required per nestling in reduced broods because of higher thermoregulatory costs (Royama 1966), especially in areas, such as ours, at relatively high latitudes with low temperatures during brood rearing (the average daily minimum temperature during brood rearing is 7.3°C (unpublished data)). It is possible that the behaviour of females was actually optimized and that they responded to the thermoregulatory needs of their young by keeping their provisioning rates at similar levels to control females. However, this seems unlikely. That females did not spend more time brooding offspring, and were more likely to remove prey from broods of reduced size, further supports our argument that they do not alter their behaviour in response to variation in brood size.

Our results suggest that female kestrels raising young employ fixed investment strategies, whereas males appear to exhibit more flexible behaviour in response to variation in brood size (Fig. 1). These results are in contrast to those from a food-manipulation study on the same population which showed that females altered their behaviour significantly when extra food was provided at nests, whereas males showed a much weaker response (Dawson and Bortolotti 2002). This study, coupled with previous results (Dawson and Bortolotti 2002), shows that the behavioural response of parents can be sex-specific and opposite, depending on the type of variable manipulated. Our study further illustrates that the contributions to parental care must be considered separately for each sex to fully understand how proximate factors affect patterns of parental investment.

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