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EFFECTS OF SHORT-TERM FOOD DEPRIVATION ON GROWTH OF HAND-REARED AMERICAN KESTRELS[1]

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Abstract. Sudden prey reductions were simulated to examine their impact on growth parameters of nestling American Kestrels (*Falco sparverius*) hand-reared in captivity. The experimental design consisted of three treatments: (1) 15 nestlings fed ad libitum (control individuals), (2) 15 nestlings that were starved for 24 hr when 7 days old, and for 36 hr when 21 days old, and (3) 15 nestlings that were starved for 36 hr when 14 days old and for 48 hr when 28 days old. Fitting biometrical data to the logistic model (body mass and the length of antebrachium, tarsus and beak) or linear models (length of the ninth primary and the central rectrix), no significant differences were found for the growth parameters of each trait between control and starved birds. This revealed no long-term effects caused by temporary starvation. Although starved individuals suffered a significant weight loss following the periods of food deprivation, they recovered mass in 2-4 days by increasing food ingestion when the ad libitum diet was restored. This flexibility of the growth of mass can be seen as an adaptive mechanism to permit compensation in day to day fluctuations of the food supply. Although American Kestrels show reversed sexual size dimorphism prior to fledging, males and females responded similarly to starvation.

Key words: American Kestrel; Falco sparverius; *raptors; growth; logistic model; starvation.*

INTRODUCTION

Intraspecific variations in avian growth rates are known to be determined by environmental factors such as diet quality and others which affect food intake of the chicks (e.g., weather, brood size, quality of parental care and hatching sequence) (Ricklefs 1983, O'Connor 1984, Bortolotti 1986, Donazar and Ceballos 1989). There have been, however, few systematic studies on the response of growth to experimentally controlled factors (Ricklefs 1983). The American Kestrel (*Falco sparverius*) is perhaps an exception, and studies have been conducted on the growth of nestlings in manipulated broods (Gard and Bird 1992), and on the effects of chronically reduced diets (Lacombe et al., in press) and different quality diets in hand-reared chicks (Lavigne 1987). A logical next step would be to determine to what extent American Kestrel nestlings can reverse abnormal growth, if any, after short-term periods of total food deprivation.

Periods of food shortage followed by others of surplus food availability can be naturally encountered by wild kestrels. Persistent bad weather may prevent the kestrel parents from hunting (Gard and Bird 1992), as seen in other raptor species (Kinaham 1975, Moss 1979, Newton 1979, Kuusela and Solonen 1984, Donazar and Ceballos 1989). Additionally, parent birds can be temporarily prevented from foraging or from feeding the chicks due to human-induced causes such as field-spraying or disturbance in the vicinity of the nest-sites.

Nestlings under starvation are known to follow different strategies (O'Connor 1978). Common swifts (*Apus apus*) apparently interrupt development (Ricklefs 1983) and can survive long periods; some species invest preferably in the growth of feathers at the expense of bone structures (Houston 1976, Boag 1987, Donazar and Ceballos 1989); others maintain bone growth at the expense of the feathers (Price 1985); and still others are not able to retard the growth of either bones or feathers (Moss 1979, O'Connor 1984). Additionally, in sexually dimorphic species, there is a potential for a differential response of the sexes to starvation.

The objectives of this study were: (1) to find out if temporary starvation causes any long-term or short-term effect on the growth of different body parts in hand-raised American Kestrels; (2) to explore whether nestling American Kestrels have any adaptive mechanism to reduce the impact of food shortages on their growth; and (3)

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to determine if male and female nestlings are affected differently by starvation.

METHODS

This experiment was conducted in 1993 at the Avian Science and Conservation Centre (McGill University, Canada), where over 300 American Kestrels are maintained in captivity. Nestlings hatched from eggs incubated naturally by kestrels breeding in outdoor pens. Techniques for keeping and breeding American Kestrels were described by Bird (1982, 1985).

The newly-hatched nestlings were color-marked and transferred to an open-air brooder where they were kept in groups of five birds that would receive the same dietary treatment. When six days old, the birds were transferred to cardboard boxes of approximately the same dimensions as nest-boxes used by free-ranging kestrels (Varland et al. 1992). When the birds were 28 days old, their average fledging time in the wild (Gard and Bird 1992), they were released into communal flight pens. The experimental design consisted of three treatments, with 15 birds each. Chicks were randomly assigned to each treatment at hatching and they were later sexed by plumage characteristics. The three treatments were the following: (A) seven males and eight females that were starved for 24 hr when seven days old, and for 36 hr when 21 days old; (B) seven males and eight females that were starved for 36 hr when 14 days old and for 48 hr when 28 days; (C) six males and nine females fed ad libitum throughout the growing period (controls). The starved birds were also fed ad libitum outside the starvation periods.

From hatching until 28 days old, nestlings were hand-fed ground day-old cockerels four times daily (except during the starvation periods) at 08:00, 12:00, 16:00 and 20:00. Body mass was recorded daily before the first meal. Once in the flight pens, the birds were given whole day-old cockerels and they were no longer hand-fed. They were then weighed when 31, 34, and 37 days old.

Linear measurements of chicks were made on the right side of the body following Olendorff (1972). The features measured were: (1) bill length to cere, (2) tarsus length, (3) antebrachium length, (4) ninth primary length, and (5) tail length (central rectrix). Measurements were taken every other day from hatching until the birds were 10 days old and every three days until 37 days old. All measurements were taken in the morning, after the first meal.

To evaluate any long-term effects of the treatments, asymptotes (A) and growth rate constants (K) of body mass, and the length of tarsus, antebrachium and beak were estimated for each individual by fitting the data to a logistic growth model (Ricklefs 1967). The Nonlin module of the statistical program "SYSTAT" (Wilkinson 1989) was used.

Data for the ninth primary and tail were fitted to a least-squares linear regression. Growth of flight feathers is not finished when the birds fledge and it is better adjusted by a linear model (Gard and Bird 1992, Viñuela and Bustamante 1992). The parameters considered for comparisons were (1) the intercept of the regression line (age at which the feather theoretically started growing), (2) the slope, or growth rate, and (3) the length when the birds were 31 days old.

To determine if significant differences existed among treatments, two-way analyses of variance (ANOVA) with sex and rearing status as factors were performed. Differences within the sexes were treated by using one-way ANOVA. Sex was considered as a factor owing to the dimorphism in body size (Gard and Bird 1992).

The short-term effects of the different starvation periods were evaluated by comparing increases in body mass, antebrachium and ninth primary length between starved birds and controls during one to three day intervals centered in the starvation periods. Increases instead of actual mass or sizes were used to avoid a possible effect of the previous starvation period during the second one.

RESULTS

EFFECTS ON BODY MASS

As a result of the starvation periods, birds in treatments A and B markedly lost mass (Fig. 1). With respect to control birds, treatment A birds lost an average of 22.7% of mass when starved for 12 hr at seven days old and about 13% when starved for 36 hr at 21 days old. Treatment B birds lost 15% of mass when starved at 14 days old (36 hr) and no loss was noticed with respect to controls when starved at 28 days old (although they lost about 10% of their previous body masses). After the starvation periods on days 7, 14 and 21, respectively, starved birds regained mass to normal values (Figs. 1A, B) in 2–4 days.

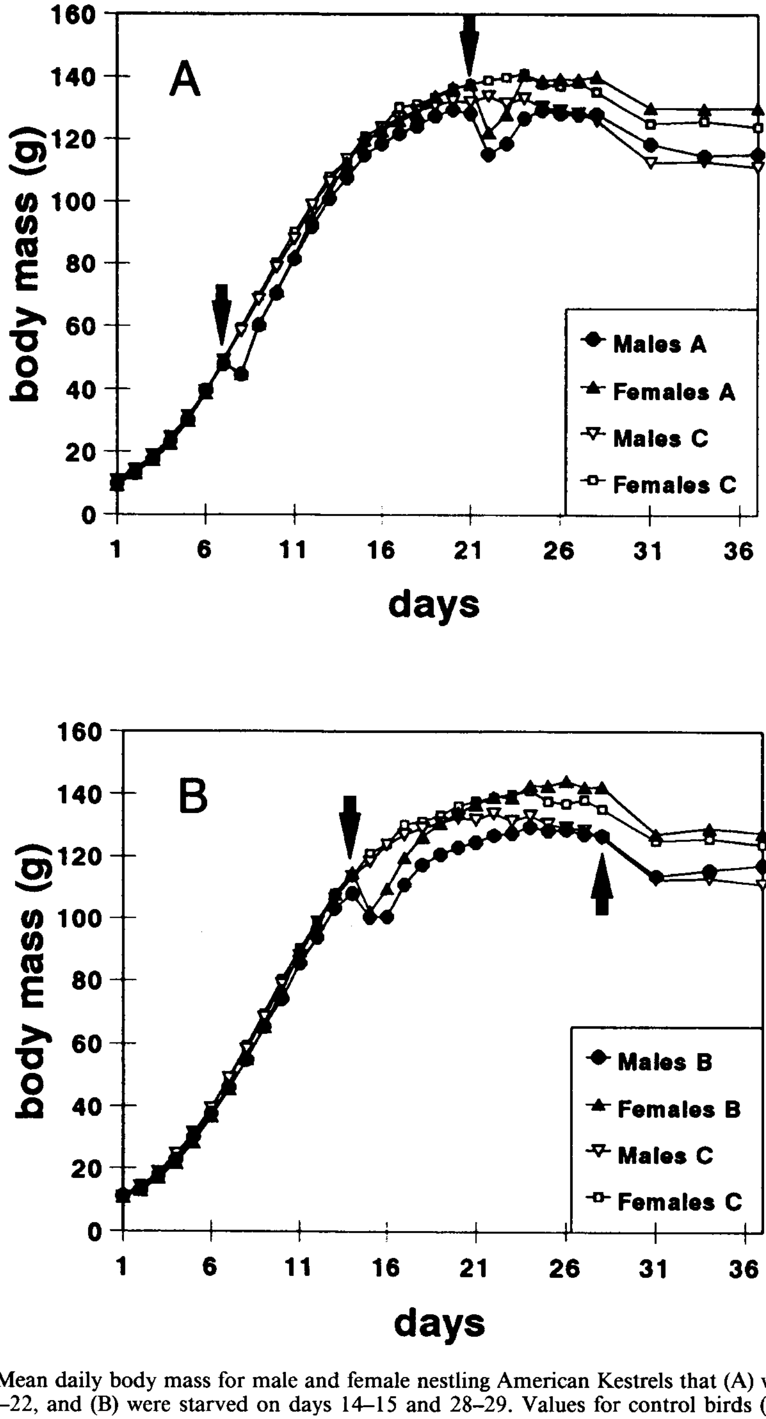


FIGURE 1. Mean daily body mass for male and female nestling American Kestrels that (A) were starved on days 7 and 21–22, and (B) were starved on days 14–15 and 28–29. Values for control birds (C) are given in graphs A and B.

Note. Hatching day = 1. Sample sizes are: A: 7 males, 8 females; B: 7 males, 8 females; C: 6 males, 9 females. Arrows indicate the start of each starvation period.

TABLE 1. Asymptotic values (A) and growth rates (K) for mass and length of antebrachium (Anteb.), tarsus and beak of starved (A, B) and control (C) nestling American kestrels (see text for description of treatments).

		Mass		Anteb.		Tarsus		Beak	
Rearing status	*n*	A (g)	K	A (mm)	K	A (mm)	K	A (mm)	K
A Males	7	125.6a	0.33ab	52.6a	0.24a	37.9a	0.24a	11.9a	0.12a
		(2.5)	(0.01)	(1.3)	(0.01)	(1.4)	(0.03)	(0.3)	(0.01)
Females	8	136.4b	0.31a	54.7b	0.23a	38.1a	0.24a	12.6a	0.12a
		(9.1)	(0.01)	(1.6)	(0.01)	(0.9)	(0.02)	(0.7)	(0.01)
B Males	7	122.8a	0.32a	51.9a	0.24a	37.0a	0.28b	12.0a	0.12a
		(3.5)	(0.02)	(0.7)	(0.01)	(0.5)	(0.02)	(0.2)	(0.01)
Females	8	136.2b	0.31a	54.8b	0.23a	37.8a	0.27ab	12.4a	0.13a
		(5.8)	(0.02)	(1.3)	(0.01)	(1.3)	(0.03)	(0.2)	(0.03)
C Males	6	127.3a	0.35b	52.1a	0.24a	37.2a	0.25a	12.5a	0.10a
		(8.2)	(0.02)	(1.2)	(0.01)	(0.5)	(0.02)	(0.3)	(0.00)
Females	9	136.8b	0.32a	54.1b	0.24a	37.3a	0.25a	12.5a	0.11a
		(6.4)	(0.02)	(1.2)	(0.01)	(1.2)	(0.03)	(0.3)	(0.01)
Two-way ANOVA factors									
Sex		***	*	***	ns	ns	ns	*	ns
Treatment		ns	*	ns	ns	ns	**	ns	*
Interac.		ns	ns	ns	ns	ns	ns	ns	ns

Note: For each variable, values within a column sharing a common letter are not significantly different at $P = 0.05$. Standard deviations are given in parentheses. * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$, ns = not significant.

The different treatments had no effects on the value of the asymptote of the growth curve (Table 1). Although females were significantly heavier than males, there were no significant differences between treatments or for the interaction between sex and treatment. Males grew slightly though significantly faster than females (see K values in Table 1). There was also a slight difference between the treatments at the limit of significance ($F = 3.36$, $P = 0.044$), due to a slower growth in males in treatments A and B.

The short-term effects of starvation were examined comparing increases in mass between starved birds and the controls (Fig. 2). Starved birds needed only two days to regain normal mass increases when starved at day 7 (Fig. 2A), four days when starved at day 14 (Fig. 2B) and four days when starved at day 21 (Fig. 2C). Coincidental with the fourth starvation period (Fig. 2D), control birds lost mass. Although the loss averaged higher for starved birds, the difference was not significant.

Starving birds ingested more food per unit of mass than controls during the days following the starvation (data not shown), and this behavior can account for the higher increases in mass.

EFFECTS ON BONE STRUCTURES

Antebrachium length. In contrast to the growth curve for mass, the antebrachium growth curves for starved and control birds are essentially the same (Fig. 3), with no obvious slow-downs after the starvation periods.

The asymptotes of the logistic growth curves for antebrachium did not differ among treatments (Table 1), although there was a marked sexual dimorphism. The growth rate was not different among treatments (Table 1), and there was no sexual dimorphism.

Increases in antebrachium length have been studied in and around the starvation periods (Fig. 4). The second starvation period for treatment B has not been considered, as the antebrachium had already finished lengthening. Only on the day after the first starvation period, starved birds showed a significantly lower increase in length for the trait than the controls. For the rest of the intervals considered, the increase of antebrachium length did not differ between starved birds and controls.

Tarsus and beak length. Asymptotic tarsus length did not show sexual dimorphism nor differences among treatments (Table 1). However, a significantly faster growth of males in treatment B was detected.

Asymptotic values for beak length did not differ among treatments (Table 1), although there was significant sexual dimorphism. In the case of the growth rate, there were differences attributable to a slightly slower growth of the control birds.

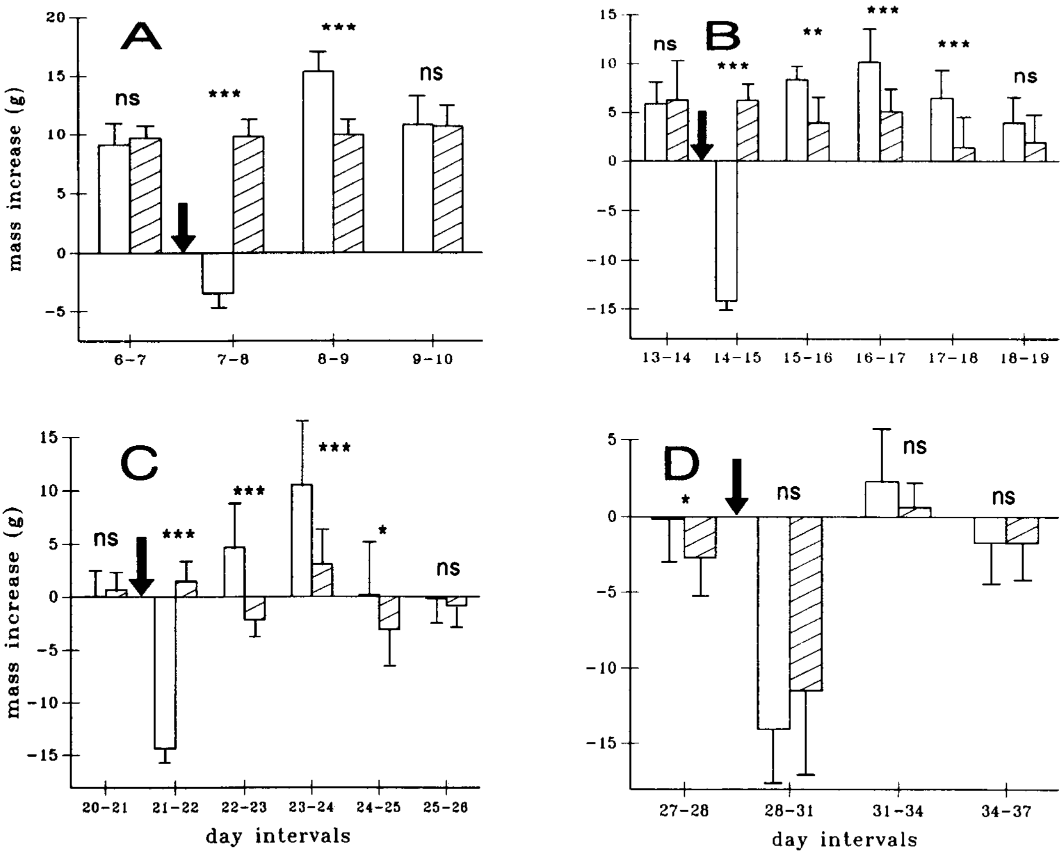


FIGURE 2. Body mass increases of starved birds (empty bars) vs. controls (hatched bars) in selected time intervals before, during and after the four starvation periods (A, B, C and D).

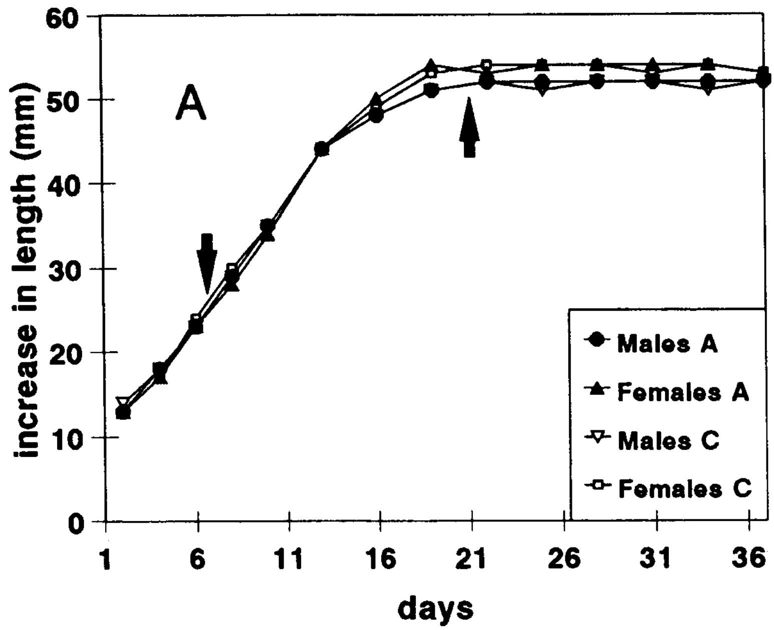
Note. Males and females have been pooled, and sample sizes are 15 for both starved and control birds. Levels of significance are given (two-way ANOVA, factor "treatment," * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$. Differences for factor "sex" were not significant, except on intervals 7–8, 14–15 and 20–21). Error bars indicate the standard deviation of the mean. The arrows indicate the start of each starvation period.

EFFECTS ON FEATHER GROWTH

The ninth primary feather grew linearly through the period of study and, as in the case of antebrachium growth, no slow-downs were noticed (Fig. 5). Nonetheless, the early sexual dimorphism shown by the control birds was almost absent in the other two groups, specially in the case of treatment A.

The intercept of the regression line on the abscissa (or the theoretical time of emergence of the feather) did not differ among treatments, and there were no sexual differences either (Table 2). This pattern holds for both the ninth primary and the central rectrix.

The slope of the regression lines (or growth rate) did not differ among treatments for either ninth primaries or rectrices, although there was significant sexual dimorphism in both traits. The length of the feather on day 31 was influenced by both the group and the sex (Table 2). Females had longer ninth primaries and rectrices than males, and birds under treatment A had shorter feathers than the others. Increases in length for the ninth primary in and around each starvation period are given in Figure 6. Starved birds showed a lower increase a few days after the first starvation period (Fig. 6A). No differences whatsoever were found after the second starvation period (Fig. 6B). Statistical differences were found during or after the third and fourth starvation periods (Figs. 6C, D), although in some cases starved birds experienced higher increases than the controls.



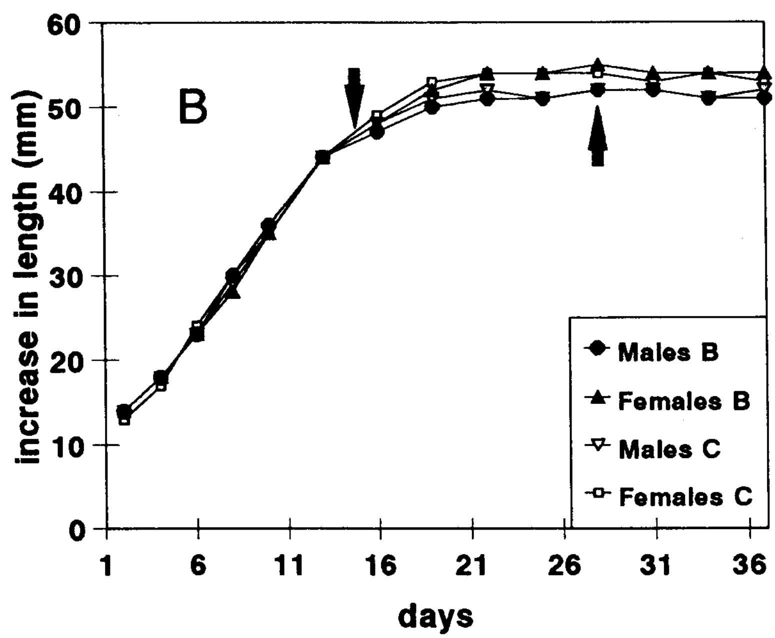


FIGURE 3. Mean daily antebrachium length for male and female nestling American Kestrels that (A) starved on days 7 and 21–22, and (B) starved on days 14–15 and 28–29. Values for control birds (C) are given in graphs A and B.

Note. Hatching date = 1. Sample sizes as in Figure 1. Arrows indicate the start of the starvation periods.

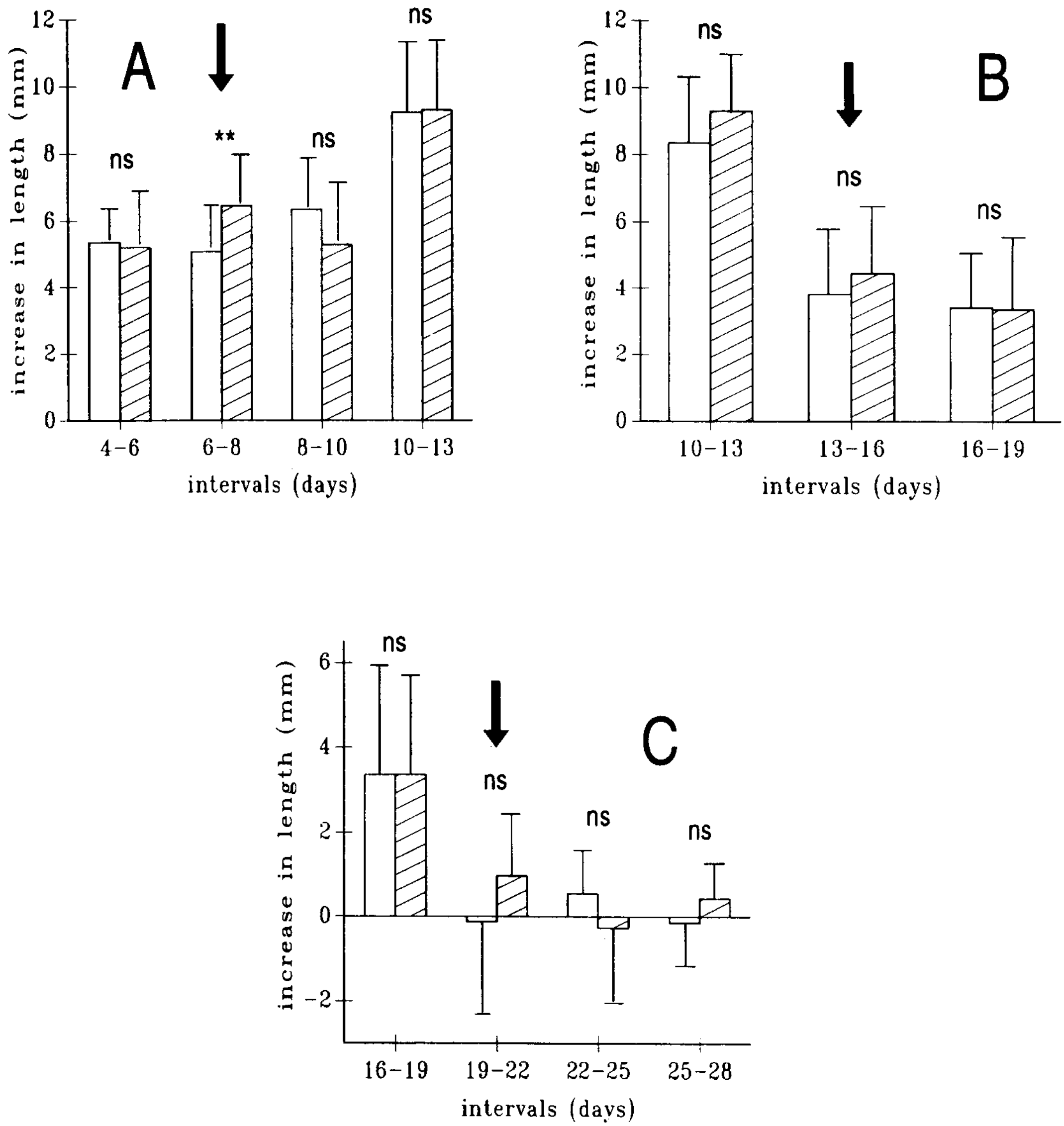


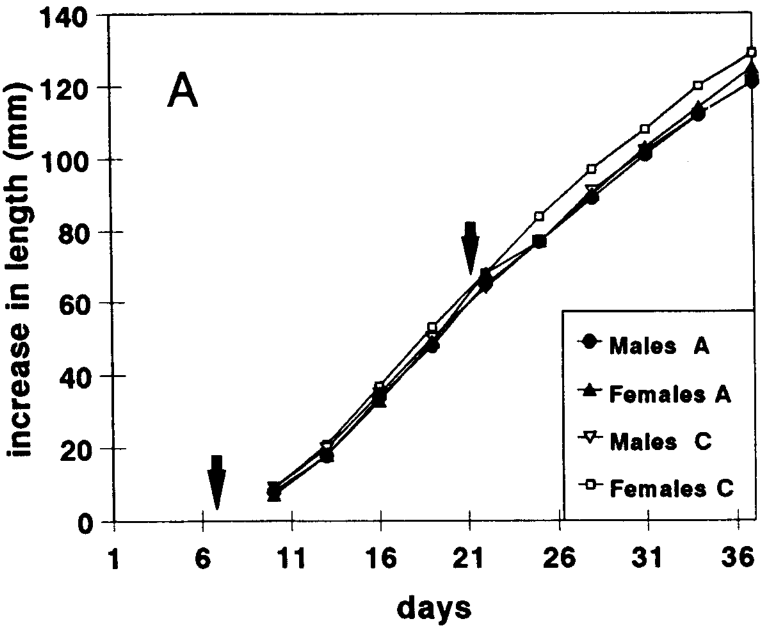
FIGURE 4. Antebrachium length increases of starved birds (empty bars) vs. controls (hatched bars) in selected time intervals before, during and after the first three starvation periods (A, B, and C).

Note. Males and females pooled, sample sizes and levels of significance for factor "treatment" as in Figure 2. Differences for factor "sex" were not significant in all cases. Error bars indicate the standard deviation of the mean. Arrows indicate the start of each starvation period.

DISCUSSION

Asymptotic masses and growth of mass for the control birds were comparable to the ones previously reported for both captive (Lacombe et al., in press) and free-ranging American Kestrels (Gard and Bird 1992). As the mean asymptotic masses did not differ among groups in our experiment, there were possibly no long-term effects of the starvation periods on body mass. The growth rate for mass, however, was slightly slower in the case of the starved birds, indicating that compensatory growth occurred to achieve the same asymptotic masses.

Given that females were larger than males since the third week of age, starvation might have af-



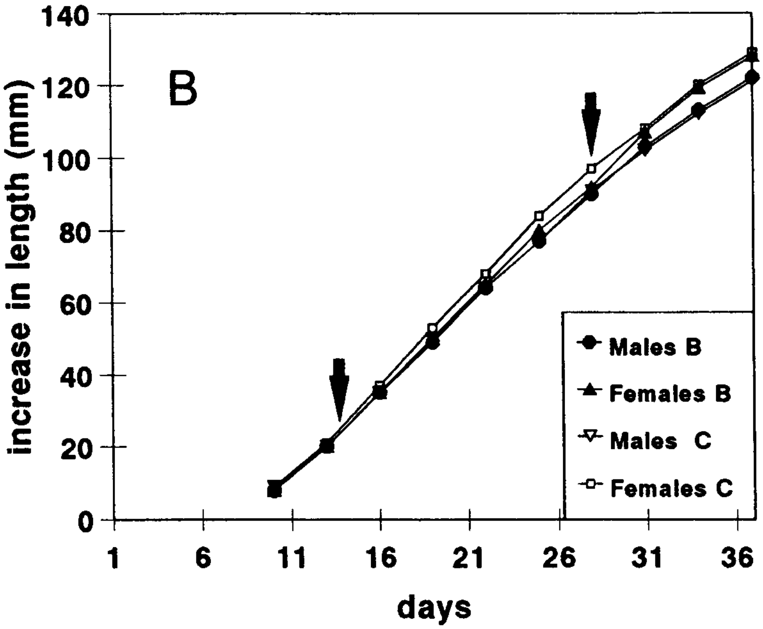


FIGURE 5. Mean daily ninth primary length for male and females nestling American Kestrels that (A) starved on days 7 and 21–22, and (B) starved on days 14–15 and 28–29. Values for control birds (C) are given in graphs A and B.

Note. Hatching date = 1. Sample sizes as in Figure 1. Arrows indicate the start of the starvation periods.

TABLE 2. Ninth primary and central rectrix day of emergency (i), growth rate (mm day^{-1}), and length (mm) at 31 days of age for starved birds (A, B) and control (C) American Kestrels (see text for description of treatments).

Rearing status	n	Ninth primary i	Ninth primary K	Ninth primary 31	Central rectrix i	Central rectrix K	Central rectrix 31
A Males	7	7.9a (0.4)	4.3a (0.1)	101.2a (2.9)	8.9a (1.8)	4.0a (0.1)	89.7a (4.5)
Females	8	8.2a (0.8)	4.4ab (0.06)	102.5a (4.4)	9.0a (1.2)	4.0a (0.2)	88.3a (2.3)
B Males	7	7.8a (0.5)	4.3a (0.1)	102.8a (2.3)	8.8a (0.6)	3.9a (0.1)	90.0a (3.5)
Females	8	8.0a (0.9)	4.5b (0.1)	107.1b (3.9)	9.6a (1.1)	4.2b (0.1)	93.6b (3.8)
C Males	6	7.5a (0.3)	4.2a (0.07)	102.0a (2.9)	8.7a (1.9)	3.9a (0.1)	90.1a (3.7)
Females	9	7.5a (0.5)	4.5b (0.1)	107.6b (3.6)	9.1a (1.0)	4.3b (0.2)	96.4b (3.5)
Two-way ANOVA factors							
Sex		ns	***	***	ns	**	**
Treatment		ns	ns	*	ns	ns	**
Interac.		ns	ns	ns	ns	*	*

Note: For each variable, values within a column sharing a common letter are not significantly different at $P = 0.05$. Standard deviations are given in parentheses. * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$, ns = not significant.

fected both sexes differentially. Losses and regains of mass went in close parallel for starved males and females though, and sexual dimorphism was expressed in the same way as in the control birds. In a previous study on kestrel growth, sexual dimorphism in mass disappeared under chronically restricted feeding (Lacombe et al., in press). The same effect was also noticed in underfed Japanese Quail (*Coturnix coturnix japonica*) (Gebhardt-Henrich and Marks 1993).

All nestling kestrels forced to fast lost mass. Young chicks suffered a higher percentage of mass loss than older chicks, even though the starvation periods were longer for older chicks. Birds that starved for 48 hr just before fledging did not lose weight significantly with respect to controls. This leads us to think that nestlings are more susceptible to starvation when they are younger. This is not surprising, as several studies reported higher mortality of nestling raptors due to starvation during the first stages of the growth period (Moss 1979, Donazar and Ceballos 1989). However, chicks starved when seven days old needed less time to regain normality than the ones starved when 14 and 21 days old.

A natural decrease in body mass around fledging time has been previously recorded in the American Kestrel (Sherman 1913, Roest 1957, Bird and Clark 1983, Lacombe et al., in press) and in many other species of birds (Ricklefs 1968a). This phenomenom has been explained as the effect of a substantial water loss when feathers and muscle mature prior to fledging (Ricklefs 1968a, 1968b). American Kestrels under a chronically restricted diet gained their asymptotic masses only at the very end of the growth period and their growth curve differed greatly from that of control birds (Lacombe et al., in press). In our experiment however, birds in all treatments peaked in mass well before fledging time, and the shape of the growth curves were similar for starved and control birds (except during the starvation periods). It is known that well-fed nestling American Kestrels store fat (Lacombe et al., in press). If feeding rates declined after fledging (as in other raptorial birds, see Bustamante 1990 and Donazar et al. 1991), the stored fat could be mobilized. This would also contribute to the decrease in body mass around fledging. The deposition of fat reserves needed for fledging or to survive temporary food shortages has already been described for passerines (O'Connor 1978).

At least after the starvation periods on days 7 and 14, in which food consumption was studied, the nestlings were able to increase their food intake, experiencing at the same time larger daily increases in mass than control birds. This considerable flexibility of growth in response to diet has already been observed in fowl (Ricklefs 1983), and in passerine birds (see "Resource storage strategy," O'Connor 1978). In precocial birds,

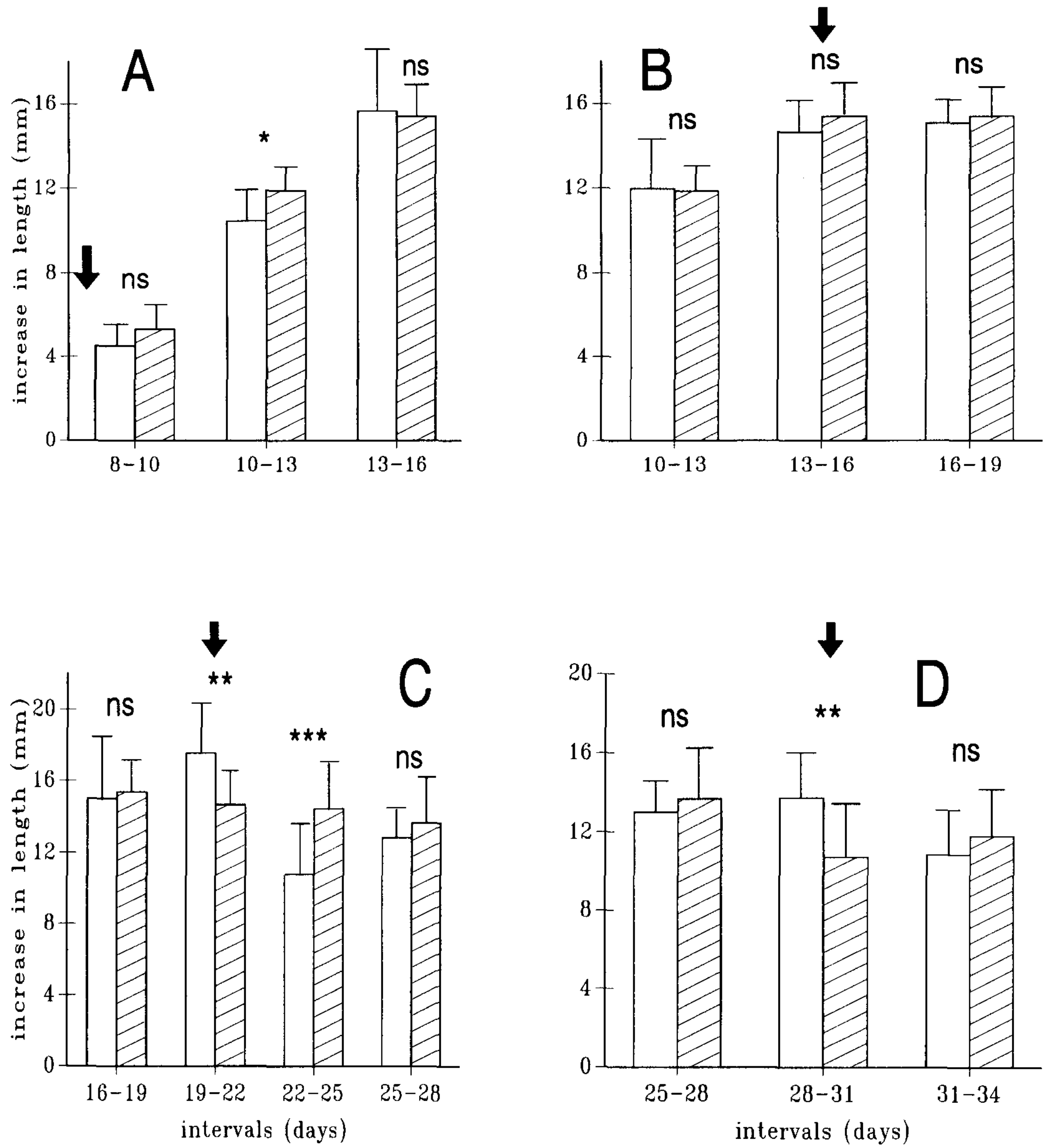


FIGURE 6. Ninth primary length increases of starved birds (empty bars) vs. controls (hatched bars) in selected time intervals before, during and after the four starvation periods (A, B, C and D).

Note. Males and females pooled, sample sizes and levels of significance as in Figure 2. Differences for factor "sex" were only significant on interval 31–34. Error bars indicate the standard deviation of the mean. Arrows indicate the start of each starvation period.

this responsiveness was explained as an adaptation of self-feeding birds to cope with variable food conditions during the growth period (Ricklefs 1983). The same logic can be applied to altricial birds. If food levels fluctuate from day to day and poor feeding periods are of relatively short duration, growth of mass is expected to be labile, permitting compensation (O'Connor 1978, 1984). In the case of semi-altricial birds of prey, including the American Kestrel (Gard and Bird 1992), brood reduction following persistent food shortage usually occurs by differential starvation of the smallest chicks (Newton 1979, O'Connor 1984). American Kestrels therefore, seem to have the potential for a "mix" of the brood reduction and the resource storage strategies, as predicted by O'Connor (1978) for birds of prey.

As with body mass, asymptotic lengths and growth rates of antebrachium, tarsus and beak did not differ between treatments in our experiment. This points to an absence of long-term effects on bone structures due to food deprivation. With regard to the short-term effects of starvation, only a decrease in the length of the antebrachium was noticed the day after the first starvation period, but it was rapidly compensated.

Some studies have found that bone measurements of raptors do not change in response to fluctuating environmental conditions (Moss 1979, Wilson et al. 1986, Korpimaki 1987). In contrast, others reported that when a reduction of feedings occurs, bone structures such as tarsus may suffer a decrease in growth rates (Houston 1976, Donazar and Ceballos 1989). In the case of the American Kestrel, most bone structures complete their growth well before the fledging time (Gard and Bird 1992, Lacombe et al., in press). An effective strategy for nestling kestrels might be to maximize growth of bone during the first weeks in the nest and then invest preferably on feathers, which continue growing for several weeks after fledging. If this were true, the two structures would compete with each other for a shorter time in the case of a food shortage.

The length of both the ninth primary and the tail in the females from treatment A was significantly shorter than those of the other two groups at day 31. "A" males also exhibited shorter feathers, but differences were not significant. Birds in treatment A suffered starvation at an earlier age (when growth of bones was peaking) than birds in treatment B, and this factor could be responsible for the difference between the two starved groups. Additionally, the second starvation period for birds in treatment B, although the longest, did not translate into a significant difference with respect to controls. Birds in treatment A therefore, seemed to have suffered from more food stress than birds in treatment B, especially the females. This reduction of sexual dimorphism in feather length, due to a depressed growth in the females, was also noticed in food-restricted Japanese Quails (Gebhard-Henrich and Marks 1993).

Shorter primaries were observed in experimentally enlarged broods of wild American Kestrels (Gard and Bird 1992) and in hand-reared nestlings under a chronically reduced diet (Lacombe et al., in press). As already mentioned, American Kestrels seem to prefer growing bone at the expense of feather when food is limited.

To summarize, starved American Kestrels showed the same asymptotic mass and length of bones as control birds. Flight feathers however, were slightly shorter in the birds that supposedly suffered a higher food stress. To what extent this can jeopardize the future survival of the young is unknown.

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