EFFECTS OF FOOD DEPRIVATION AND HANDLING STRESS ON FAULT-BAR FORMATION IN NESTLING AMERICAN KESTRELS *Falco sparverius*

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ABSTRACT We document the extent of fault-bar formation in the wing and tail feathers of 45 hand-reared and 18 parentally reared American Kestrels *Falco sparverius* raised in captivity on temporarily interrupted (30 birds) and uninterrupted (15 birds) ad libitum diets. Hand-reared birds were handled extensively throughout the experiment, parentally reared birds were not. Hand-reared nestlings developed an average of 2.8, 8.0 and 4.3 and parentally reared nestlings an average of 0.6, 1.4 and 0.4 fault bars on their rectrices, primaries and secondaries, respectively. All hand-reared birds, including the group whose diet was not interrupted, had significantly more fault bars on their rectrices, primaries and secondaries, than did parentally reared birds. Fault-bar formation in birds whose ad libitum diets were interrupted did not increase at times of food deprivation and hand-reared birds from which ad libitum food had been withheld for 24 to 48 hours did not have more fault bars than hand-reared birds whose diets had not been interrupted. Our results suggest that excessive fault-bar formation in captive birds is most likely due to handling stress, rather than to food deprivation.

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INTRODUCTION

Fault bars are narrow, frayed bands that occur in the feathers of many birds (Riddle 1908, Stiefel 1985, Machmer *et al.* 1992). The result of abnormally formed or missing barbules (King & Murphy 1984), fault bars weaken feathers, making breakage more likely (Hawfield 1986, Newton 1986).

Fault bars are perhaps best known in Falconiforms, where their occurrence is well documented, both in the falconry (Lascelles 1892, Evans 1960, Glasier 1978) and scientific literature (Hamerstrom 1967, Hawfield 1986, Newton 1986, Machmer *et al.* 1992). The causes of such feather defects remain unclear. Long suspected of being associated with nutrition stress during feather growth (Stiefel 1985), fault bars are sometimes refered to as "hunger traces" (Lascelles 1892, Beebe & Webster 1964) or "hunger streaks" (Michell 1900, Hamerstrom 1967). Recent evidence suggests that stress related to handling (King & Murphy 1984, Murphy *et al.* 1988, Murphy *et al.* 1989) is responsible for the formation of fault bars in captive birds. A field study by Machmer *et al.* (1992) on nestling Ospreys *Pandion haliaetus* reported evidence in support of both handling and food stress.

Here, we present data from a controlled laboratory experiment aimed at comparing the roles of food deprivation and handling in the formation of fault bars in the wing and tail feathers of nestling American Kestrels (*Falco sparverius*).

METHODS

Our experiment was conducted at the Avian Sci-

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ence and Conservation Centre (McGill University, Canada) where over 300 American Kestrels are maintained in captivity (Bird 1982). Nestlings used in the experiment hatched from eggs incubated naturally by kestrels breeding in outdoor pens.

The effect of food deprivation on fault-bar formation was tested by hand-rearing three treatment groups (A, B and C) of 15 kestrels each on different food regimes, two in which food was twice withheld and one in which food was not withheld (see below). The effect of handling on fault-bar formation was tested by comparing the numbers of fault bars in hand-reared nestlings in treatment groups A, B and C, all of which had been handled extensively throughout the experiment, with that of a fourth group of 18 parentally reared nestlings (6 broods of 3 each) that were not handled during the period of feather growth.

At hatching, 45 nestlings were transferred to incubators where they were hand-reared on an ad libitum diet of ground day-old cockerels 4 times daily (except as mentioned below) at 08:00, 12:00, 16:00 and 20:00. When 6 days old, the nestlings were transferred to cardboard boxes of approximately the same dimensions (0.25 x 0.25 x 0.40 m, LxWxH) as nest boxes used by free-ranging kestrels (Varland *et al.* 1992). When the kestrels were 28 days old, they were moved to flight pens, where day-old cockerels were available on an ad libitum basis. The 15 birds (7 males, 8 females) in treatment A received ad libitum food on all days except for 24 hours beginning on day 7 and for 36 hours beginning on day 21. The 15 birds (7, 8) in treatment B received food every day except for 36 hours beginning on day 14 and for 48 hours beginning on day 28. The 15 birds (7, 8) in treatment C received food every day. The adult kestrels that raised the 18 nestlings (5, 13) in treatment D were fed cockerels ad libitum once a day.

All hand-reared birds were weighed once daily until 28 days of age, and then every three days until they were 37 days of age. Linear measures of growth (beak, antebrachium, tarsus, 9th primary, tail) were made on alternate days through day 10 and every three days until day 37. Handling time averaged 5 min per bird.

The number of fault bars in flight feathers was recorded when the birds were 39 days old. The location of each fault bar with respect to the distal end of each feather was measured. Feathers were examined indoors under a fluorescent lamp by a single observer (JJN) with an unaided eye. The date of fault-bar formation was estimated for all fault bars in rectrices using the following equation:

$$Date = ARE + (BD \cdot GR^{-1})$$

where *Date* is the date of fault-bar formation in days since hatching, *ARE* is chick age in days at the time the feather erupted, *BD* is the distance of the fault bar to the distal end of the feather in mm, and *GR* is the mean daily growth rate in mm of rectrices. The date of rectrix eruption (approximately 9 days of age) was predicted by regressing tail length on age.

RESULTS

A total of 726 fault bars was observed in the rectrices (137), primaries (389) and secondaries (200) of the 63 nestling American Kestrels we studied. Within each of the four treatments, fault-bar frequency did not differ significantly between genders (Mann-Whitney U tests, $P > 0.05$). Consequently, data from males and females have been pooled in subsequent analyses. Mean numbers of fault bars in the different plumage groups (rectrices, primaries, secondaries) for each treatment are presented in Table 1. Fault-bar frequency did not differ among nestlings in any of the three hand-reared treatments in any plumage group. However, kestrels in each of the three hand-reared groups had significantly higher numbers of fault bars in each plumage group than did parentally reared nestlings (Table 1). These results indicate that differences in the extent to which the captive birds were handled had a greater effect on fault-bar formation than did withholding food for periods of from 24 to 48 h.

Table 1. Mean numbers per nestling and standard deviations (*SD*) of fault bars in the rectrices, primaries and secondaries of nestling American Kestrels reared in captivity.

		Mean number of fault bars ± *SD*		
Treatment	*n*	Rectrices	Primaries	Secondaries
A*	15	2.2 ± 3.2a** (0.18)a***	7.9 ± 6.3a (0.39)b	5.2 ± 3.9a (0.21)a
B	15	2.6 ± 3.8a (0.21)a	8.8 ± 3.9a (0.44)b	4.0 ± 2.8a (0.16)a
C	15	3.6 ± 3.6a (0.30)ab	7.4 ± 4.8a (0.37)b	3.6 ± 3.5a (0.15)a
D	18	0.6 ± 1.6b (0.05)a	1.4 ± 1.6b (0.07)b	0.4 ± 0.6b (0.01)a

*A = Hand-reared, ad libitum diet, food withheld for 24 h (day 7) and 36 h (day 21). B = Hand-reared, ad libitum diet, food withheld for 36 h (day 14) and 48 h (day 28). C = Hand-reared, ad libitum diet, food not withheld. D = Parentally reared, ad libitum diet, food not withheld. **Values within columns sharing a common letter are not significantly different from one another ($P < 0.05$, Mann-Whitney *U* tests). ***Parenthetical numbers indicate mean number of bars per feather. Values within rows sharing a common letter are not significantly different from one another ($P < 0.05$, Mann-Whitney *U* tests).

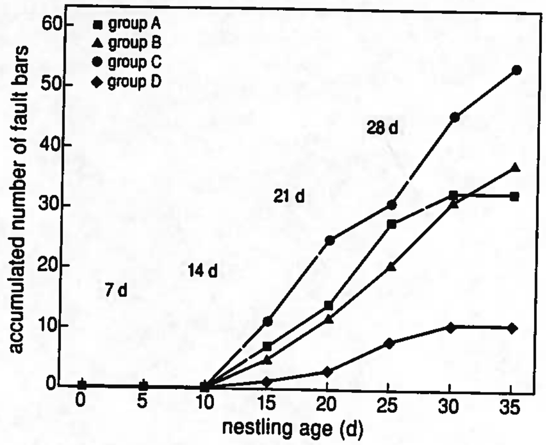

Fig. 1. Fault-bar formation in the rectrices of nestling American Kestrels as a function of age. Lines represent accumulated numbers of fault bars from all the birds in each experimental group· Arrows indicate periods when food was not available to birds in treatments A and B.

Although there were differences in the timing of fault-bar formation in the rectrices of birds within the four treatment groups, periods of food withdrawal did not increase the rates at which fault bars were formed in birds in treatments A or B (Fig. 1).

A multiple-rank correlation of the number of fault bars in the primaries, secondaries and rectrices of individual birds indicated that fault-bar formation was not consistent among plumage groups within individuals. For example, while the frequency of fault bars in primaries was weakly, though significantly associated with fault-bar formation in secondaries (Spearman's $r = 0.33$, $n = 63$, $P < 0.05$), fault-bar formation in rectrices was not correlated with fault-bar formation in either primaries ($r = -0.09$, $n = 63$, $P > 0.05$), or secondaries ($r = -0.12$, $n = 63$, $P > 0.05$). These results suggest that fault-bar formation in wing and tail feathers may result from different causes.

The numbers of fault bars on the left and right sides of the tails of individual birds were not significantly correlated ($r = 0.24$, $n = 63$, $P > 0.05$). However, there were significant correlations between right-side and left-side fault-bar formation, both in primaries ($r = 0.54$, $n = 63$, $P < 0.01$) and secondaries ($r = 0.42$, $n = 63$, $P < 0.01$). Visual inspection of the feather charts of individual birds however, revealed little, if any, left-right symmetry in fault-bar formation on a matching feather basis in any plumage group.

DISCUSSION

Our experiments fail to demonstrate a link between acute food deprivation and fault-bar formation in hand-reared nestling American Kestrels. On the other hand, our results suggest a link between "physical stress" (i.e., handling nestlings on a regular basis) and increased fault-bar formation. Overall, our results support earlier studies of the similar relationships in captive White-crowned Sparrows, *Zonotrichia leucophrys*, King & Murphy 1984, Murphy *et al.* 1988, 1989) and Ring-necked Pheasants, *Phasianus colchicus*, Solomon & Linder 1978).

Other studies of fault-bar formation in captive birds (Riddle 1908; Melius 1975), as well as a number of field studies of free-ranging individuals (Hamerstrom 1967, Stiefel 1985, Hawfield 1986, Newton 1986, Waite 1990, Machmer *et al.* 1992) have suggested a link between fault-bar formation and food shortages in raptors and other species. In most instances the supposed link was based on increased fault-bar formation in free-ranging birds whose food supply had likely been interrupted or reduced, either as a result of foul weather, reduced prey availability, or sibling competition.

Hand-rearing the birds did not retard their growth. With the exception of substantial weight losses (15-23% compared to controls, Negro *et al.* 1994) following periods of food deprivation, the ultimate growth performance of hand-reared birds did not differ from that of captive and free-ranging parent-reared birds (Negro *et al.* 1994, Gard & Bird 1992).

We suggest that the inability of researchers such as ourselves to demonstrate in controlled captive situations what appears to be occurring in the field results from the fact that nutritional stress in free ranging birds typically co-occurs with other forms of stress as well. As an example, nestlings that are starving because rain has interrupted the hunting behaviour of their parents (cf. Newton 1986) may be both thermally and physically stressed. In addition, the lack of symmetry in the number of fault bars in the right and left sides of the tails suggests random occurrence with no relation to the starvation periods, which occurred at fixed days.

Despite considerable individual variation, our results suggest that fault bars are more likely to occur in the primaries of developing American Kestrels, than in their secondaries or rectrices (Table 1). In contrast, previous studies of fault bars, both in raptors and other species of birds, suggest that the feather defects are more common, more pronounced, or both, on rectrices than on flight feathers (Hamerstrom 1967, Slagsvold 1982, King & Murphy 1984, Hawfield 1986, Murphy *et al.* 1988, 1989, Machmer *et al.* 1992), or that they are equally common on primaries and secondaries (Solomon & Linder 1978). The hand-reared and parent-reared American Kestrels we studied developed in the confined space of a "nest-box." Outer flight feathers on the wings of nestlings attempting to flex their wings in such spaces would more likely to come into physical contact with barriers (the walls of the nest box), than would birds in species developing in open nests. If such events induced fault-bar formation, nestling kestrels would have a greater numbers of fault bars on primaries than would open-nesting species.

Whatever their exact cause or causes, fault bars occur regularly enough in free-ranging raptors (cf. Hawfield 1986, Newton 1986) and possibly other species of birds (Stiefel 1985), to make them potentially useful indicators of the degree of stressful conditions in an individual's recent past. Similarly, possible variability in their occurrence between genders, among age classes and across geographic regions would enable researchers to compare stress levels in within and among populations (Slagsvold 1982). Given the potential benefits of their use, additional studies of their occurrence in natural populations and specific causation in captive populations appear to be merited.

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SAMENVATTING

In dit artikel wordt een experiment beschreven waarin de invloed wordt nagegaan van voedselgebrek en het hanteren (door mensen voor onderzoek) op de vorming van zogenaamde faultbars (veerafwijkingen) bij nestjongen van de Amerikaanse Torenvalk. Faultbars zijn lichte smalle dwarsstrepen in een veer, veroorzaakt door een verstoorde ontwikkeling van de baardjes tijdens de groei van de veer.

Sommige jongen werden met de hand grootgebracht en sommigen door hun ouders. De met de hand grootgebrachte jongen ontwikkelden aanzienlijk meer faultbars in hun grote en kleine slagpennen en staartpennen dan de jongen die door hun ouders waren grootgebracht.

Er kon geen invloed worden aangetoond van het onthouden van voedsel gedurende 24-48 uur op de vorming van faultbars. Kennelijk is de nogal buitensporige ontwikkeling van faultbars bij vogels in gevangenschap meer het gevolg van hanteren – en wellicht de stress die daarmee gepaard gaat – dan van schommelingen in het voedselaanbod.

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