Fault Bars in the Feathers of White-crowned Sparrows: Dietary Deficiency or Stress of Captivity and Handling?

JAMES R. KING AND MARY E. MURPHY
Department of Zoology, Washington State University, Pullman, Washington 99164 USA

Fault bars are translucent bands in feathers, typically a millimeter or less wide in small songbirds, approximately perpendicular to the rachis. They are caused by the defective formation of barbules. They should not be confused with "growth bars," which are wider bands of contrasting diffraction corresponding to daily growth (Michener and Michener 1938, Wood 1950, Lüdicke and Gierhaas 1963). Riddle (1908) was apparently the first investigator to study the occurrence of fault bars experimentally, and he concluded on the basis of evidence that now seems tenuous that they resulted from malnutrition. Michener and Michener (1938) suggested that fault bars in passerines ("bands" in their terminology) resulted from some type of "metabolic deficiency." Melius (1975) thought that the bars were caused by "stressful conditions," including restricted food intake, in Ring-necked Pheasants (*Phasianus colchicus*). Solomon and Linder (1978), on the other hand, found no correlations between the incidence of fault bars and food deprivation or the supposed stresses of crowding in this species. These investigations have not clearly identified the cause or causes of fault bars.

As a by-product of investigations of the effects of dietary sulfur-containing amino acids (SAA = cystine and methionine) on feather formation during postnuptial molt in White-crowned Sparrows (*Zonotrichia leucophrys gambelii*), we recorded the incidence of fault bars and report herewith the correlations or lack thereof that we found between fault bars and dietary concentrations of SAA and other conditions of husbandry. As we will show, fault bars are correlated with the frequency with which the birds were handled but not with the quality of the diets that we supplied.

About 1 month before postnuptial molt began, we transferred two groups of White-crowned Sparrows from chick-starter mash to semi-synthetic diets (Murphy and King 1982) that were isocaloric (17.40 kJ/g dry wt.) and isonitrogenous (13.5% protein by dry wt.) but that differed in SAA concentration. Diet A contained 2.15% of protein as SAA, and Diet B contained 6.43%. This approximates the range of SAA concentration found in natural diets, and diets A and B would be regarded as marginal or deficient and super-adequate, respectively, in this context (Murphy and King 1984). The birds were housed individually in small cages (22 × 40 × 27 cm), fed and watered daily, and were weighed and inspected for the condition of molt every sixth day. They remained on the experimental diets throughout the molt and postmolt periods. We show elsewhere (Murphy and King 1984) that the rate of molt and the mass of the renewed plumage were normal (compared with birds fed chick-starter mash) and were statistically indistinguishable in groups A and B.

The incidence of fault bars in the rectrices and the distance between them were alike in the two groups (Table 1), which suggests that fault bars were not attributable to low SAA concentration in the diet. The pooled mean distance between fault bars in groups A and B was 20.6 ± 0.54 mm (62 intervals). At an average growth rate of 3.5 mm/day (Murphy and King 1984), this corresponds to 5.9 days. We handled these birds at intervals of 6 days, give or take about 2 h, to weigh them and record the status of molt. This coincidence prompted us to measure the distance between fault bars in three White-crowned Sparrows that we had, by chance, preserved from a parallel experiment in which the living conditions were essentially identical to those in groups A and B except that the birds were handled every third day. The mean distance between fault bars in these birds was 11.1 ± 0.29 mm (11 intervals), which corresponds to a mean of 3.2 days. These correlations suggest that it is the trauma of handling that induced the formation of fault bars. Several lines of indirect evidence support this conclusion. (1) Fault bars were rare in White-crowned Sparrows that molted in large aviaries with minimal disturbance (mean number of fault bars/tail = 0.75, $n = 12$ birds) and in White-crowned Sparrows caught during autumn migration (0.25 fault bars/tail, $n = 12$ birds). These frequencies are more than an order of magnitude less than in the experimental birds (Table 1). (2) It would be predicted from the nutritional deficiency hypothesis that fault bars would be either more frequent in wild birds than (if their diets were variable and susceptible to shortages) or the same as (if their diets were always adequate) in experimental birds that were fed an adequate diet. The converse is true. (3) Fault bars are of nearly uniform width, corresponding to about 6–8 h of normal growth at an average rate. It seems unlikely that dietary deficiencies would be uniform enough to produce this small range of variation. On the other hand, it is plausible that the period of neural or neuroendocrine recovery from the trauma of handling would be relatively uniform. (4) The differential distribution of fault bars in the flight feathers favors a neural or neuroendocrine mediation. As shown in Table 1, fault bars are much more common in rectrices than in remiges. Furthermore, 68% of the fault bars in remiges occurred in the tertials (secondaries 7, 8, and 9) in White-crowned Sparrows, although only 33% would be expected on the basis of chance. It seems unlikely that blood-borne nutrient

TABLE 1. Frequency of fault bars and the distance between bars in White-crowned Sparrows fed low (Group A) and high (Group B) concentrations of sulfur-containing amino acids.

Dietary group	Mean (± SE) number of fault bars in[a]		Mean (± SE, mm) distance between rectricial bars
	Tail	Wings	
A ($n = 5$)	15.2 ± 3.97[b]	5.0 ± 1.47[c]	20.2 ± 0.56[d]
B ($n = 4$)	17.5 ± 3.93[b]	6.8 ± 2.63[c]	20.9 ± 0.90[d]

[a] 12 rectrices or 36 remiges per bird.
[b] $P = 0.35$ that means differ (paired t-test, df = 7).
[c] $P = 0.30$ that means differ (paired t-test, df = 7).
[d] $P = 0.26$ that means differ [df = 60 (62 intervals in 46 rectrices)].

supply could account for this differential susceptibility. We think that the weight of evidence strongly favors the shock of handling as the cause of fault bars in captive birds, and presumably some similar shock (such as flight from a predator) causes them in free-living birds. Many episodes of handling did not result in fault-bar formation in the captives, however, which suggests that the underlying mechanism has a variable threshold and may be multifactorial.

Finally, we offer the outright speculation that fault bars are a mild form of the response to shock that produces "fright molt" (*Schreckmauser*: Dathe 1955, Juhn 1957). Fright molt is the essentially instantaneous shedding of feathers by birds that are thought to be frightened or subjected to stress (*Angst*: Dathe 1955) and is probably the analog of the autotomy of body parts by which organisms of several taxa distract predators (for review, see Dial and Fitzpatrick 1983). External mechanical forces are not involved in the reaction. Dathe (1955) cites records from 52 species in 15 families and 7 orders of birds. Tail feathers are most commonly shed, followed less commonly by body feathers and wing feathers. We did not examine body feathers for fault bars in our experiments, but it is noteworthy that rectrices are more susceptible to fault bars, and to fright molt, than remiges. Although Dathe (1955) reports that only mature feathers are shed during fright molt, while growing feathers in the same bird are not, it is not known whether or not fault bars are formed in the latter at the time of a fright molt. Dathe discussed the possibility that the expulsion of a feather from its papilla is caused by either a sudden relaxation of the feather muscles or a sudden contraction, but he was unable to reach a conclusion. If fright molt and fault-bar formation are really two gradations of the same process, it seems more likely that muscular contraction is the causative force. A relatively mild, prolonged contraction might cause an ischemia preventing the flow of nutrients and regulatory chemicals to an active follicle, thus producing a fault bar, while a more violent contraction might expel a feather from its follicle. Furthermore, it is more plausible that a hardened feather would be expelled than a soft, growing feather in which some of the muscular force would be absorbed by elasticity.

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