

# Frequency of fault bars in feathers of birds and susceptibility to predation

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Fault bars are transparent bands in the feathers of birds produced under stressful and adverse conditions. The frequency of feathers with fault bars is highly heterogeneous among species. We predicted that prey had a higher frequency of fault bars than individuals from the general population, and that a high susceptibility to predation would be associated with a low frequency of fault bars among species of birds because such species would suffer particularly high costs of producing fault bars. The frequency of fault bars in prey was almost three-fold higher than in the general population, based on a database on the frequency of fault bars and susceptibility to predation by the goshawk *Accipiter gentilis* L., implying intense natural selection against fault bars. A high susceptibility to predation by the sparrowhawk *Accipiter nisus* L. and the goshawk, relative to what would be expected from their abundance, was associated with a low frequency of fault bars across species, with long distance migration also being negatively associated with frequency of fault bars. Feathers with fault bars were more likely to break than feathers without fault bars, thereby potentially affecting the flight ability of individuals. These findings are consistent with the hypothesis that susceptibility to factors that cause production of fault bars can be modified by natural selection, as illustrated by the impact of predation on the frequency of fault bars. © 2009 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2009, 97, 334–345.

ADDITIONAL KEYWORDS: developmental control – feathers – moult – risk – stress.

## INTRODUCTION

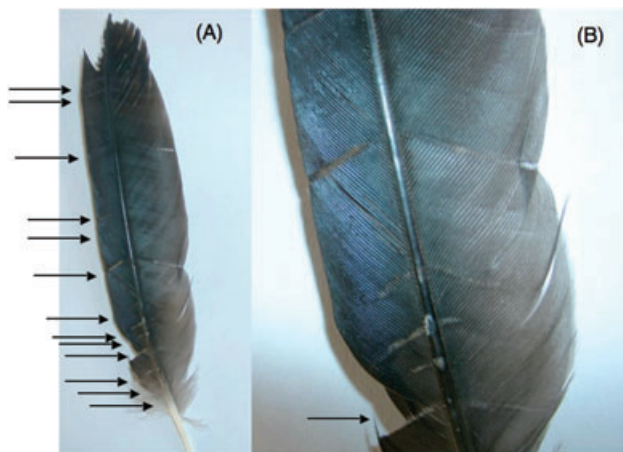
Moulting in birds occurs as a sequence of daily growth increments, producing so-called growth bars with a dark and light part during day and night, respectively, readily discerned on many feathers with the naked eye (Fig. 1) (Ginn & Melville, 1983; Svensson, 1984). Sometimes, such daily growth increments may fail due to lack of barbule cell development in an 'isochronic' section of cells within a set of barb ridges, causing all feather barbs produced during that specific daily growth increment to be almost transparent and hence weakened (Michener & Michener, 1938; Wood, 1950; Møller, Kimball & Erritzøe, 1996; Prum

& Williamson, 2001; Blanco & de la Puente, 2002; Bortolotti, Dawson & Murza, 2002; Jovani & Tella, 2004). Fault bars are clearly visible to the naked eye as a transparent band perpendicular to the longitudinal axis of the feather (Fig. 1).

Fault bars cause feathers to be weakened and therefore have elevated risk of breakage. Why would an individual not only produce feathers without fault bars? First, developmental control that could prevent production of fault bars may differ among individuals and species, and, second, species may differ in susceptibility to factors that cause fault bars because the cost of fault bars differs among individuals and species.

Any developmental mechanism that assured constant deposition of keratin and pigments into feathers would result in the production of feathers of homogeneous quality. Such mechanisms could be perturbed

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**Figure 1.** Photograph of a tail feather of a carrion crow *Corvus corone corone* showing (A) the clearly visible 13 fault bars (at the arrows) and (B) feather breakage at a fault bar (at the arrow). Photograph by J. Erritzøe.

by availability of biochemicals for feather production or stress, as suggested by experiments by Murphy, Miller & King (1988, 1989) and Murphy & King (1984). Stressful conditions cause fault bars to develop as shown by experiments that have manipulated the size of secondary sexual characters, the frequency of handling by experimenters, food availability, and access to safe shelter (Møller, 1989; Machmer *et al.*, 1992; Negro, Bildstein & Bird, 1994; Witter & Lee, 1995; Whitmore & Marzluff, 1998). Adverse environmental conditions or low body condition are associated with the presence of fault bars, although not all studies have shown such an effect (Møller *et al.*, 1996; Blanco & de la Puente, 2002; Bortolotti *et al.*, 2002; Jovani & Tella, 2004).

Susceptibility to factors that cause fault bars differs among individuals and species because the cost of fault bars differs. Fast moulting would reduce the duration of the moult, but speed would come at the cost of potential production of feathers of low quality, if biochemicals needed to produce feathers were limiting. Thus, individuals must optimize the timing and speed of moulting to minimize risk of production of fault bars, at the same time as not sacrificing fitness due to late start of reproduction caused by an extended moult period. This optimization problem could affect susceptibility to factors that cause development of fault bars. Consistently, fault bars are distributed strategically among feathers relative to their importance for flight, with fault bars being rare in the aerodynamically most important feathers, suggesting that susceptibility to factors causing fault bars for different feathers has been modified to minimize the risk of production errors (Jovani & Blas, 2004). Feathers with fault bars have been hypoth-

esized to be more likely to break than feathers without bars (Kose, Mänd & Møller, 1999; Dawson, Bortolotti & Murza, 2001), and this critical assumption has been supported by an elevated frequency of feather breakage at fault bars (Sarasola & Jovani, 2006). Such feather breakage would impair flight because holes in wings and tails seriously affect aerodynamics (Norberg, 1990), independent of whether feathers are missing because of feather breakage or moulting (Swaddle *et al.*, 1996). However, the aerodynamic effects of fault bars are more severe than those caused by the moult because moulting proceeds symmetrically on the two sides of the body (Ginn & Melville, 1983), whereas the position of fault bars is hardly ever symmetric (own observations). Experiments have shown that asymmetry in feather length affects flight ability (Møller, 1991; Swaddle *et al.*, 1996). Such impaired flight caused by fault bars can potentially affect foraging efficiency, the quality of aerial sexual display, migration ability, and the ability to escape predators. For example, experimental increase in tail length of male barn swallows *Hirundo rustica* L. caused an increase in the frequency of fault bars after the subsequent moult (Møller, 1989). In addition, the frequency of fault bars was strongly negatively related to natural variation in tail length of male barn swallows, demonstrating that long-tailed males were in better condition, as reflected by their lower frequency of fault bars than naturally short-tailed males (Møller, 1994). Migration by birds often covers distances that exceed 10 000 km twice annually, resulting in very large energy expenditure (Berthold, 2001). Therefore, there is intense natural selection on morphology and behaviour to reduce costs of migration. Similarly, predation accounts for a large fraction of mortality across taxa (Curio, 1976), causing natural selection to act on flight morphology and behaviour that reduce such costs of natural selection. A higher prevalence of fault bars should lead to a greater frequency of asymmetric feather breakage, which in turn could decrease individual agility and hence the ability to escape predators. Any of these costs could affect either developmental control of feathers or susceptibility to factors that cause fault bars to develop.

The present study aimed to assess how presence of fault bars was traded against predation risk, and other ecological factors. We predicted that: (1) the frequency of fault bars differ among individuals and species; (2) the risk of feather breakage at fault bars is greater than expected by chance; (3) the frequency of fault bars is higher among individuals that eventually become prey than in the general population; and (4) there is a negative relationship between risk of predation and frequency of fault bars across species because fault bars should be particularly costly in

species with a high risk of predation. Such proximate patterns that reflect underlying mechanisms often differ from ultimate patterns that reflect evolutionary relationships (Martin, Scott & Menge, 2000). These predictions were tested using extensive data collected over a period of 30 years from 86 bird species.

## MATERIAL AND METHODS

### FREQUENCY OF FAULT BARS

Undamaged specimens were investigated that had been received by one of the investigators (J.E.) when he was a taxidermist in Christiansfeld, Denmark, during 1975–2005. Specimens were received throughout the year, with largest numbers in late summer just after the breeding season. Primaries, secondaries and rectrices were carefully inspected against a light source and the number of fault bars counted as the number of clearly transparent bars as shown in Figure 1A. Although feather discontinuities vary from clear weaknesses with a width of more than 2 mm to faint weak bands, only wide and clearly visible bars, as shown in Figure 1A, were scored. We obtained two estimates of the abundance of fault bars: (1) the mean number of fault bars on individuals with fault bars and (2) the proportion of individuals having fault bars. Although data were available for a very large sample of species, we restricted the present analysis to species for which there was data available for at least five specimens. Because there was still considerable variation in sample size among species (5–351), we tested for the effect of sample size by also weighting analyses by sample size to control for differences in sampling effort (see Statistical analysis). Danish law requires all specimens delivered to taxidermists to be listed in an official protocol with explicit information on cause of death, date, locality, and finder, and this information was recorder meticulously throughout the study (by J.E.). Most specimens investigated are currently available in the collection of J. Erritzøe (<http://www.birdresearch.dk>).

We tested whether different persons recorded fault bars repeatably, by letting two individuals (A.P.M. & A. C. Møller) independently record fault bars in 2820 feathers of 235 goshawk prey (see below). The second observer was unaware of the purpose of the study and also unfamiliar with birds in general. This exercise produced the same 56 individuals with fault bars, showing that fault bars could be identified unambiguously.

Finally, we explicitly tested whether estimates of the frequency of individuals with fault bars based on the sample from J.E. were reproducible by using data from a second independent source; field samples of live birds captured in mist nets by A.P.M. in Northern

Jutland, Denmark 1975–2003. Thus there was no reason to expect that the samples recorded by A.P.M. differed in seasonality from those recorded by J.E. A.P.M. used exactly the same procedure as J.E. in assessing frequency of fault bars in primaries, secondaries and rectrices. Pairs of estimates for the 15 species with the largest sample sizes are reported in the Supporting information (Appendix S1). A paired *t*-test of square-root arcsine-transformed estimates did not reveal a significant difference ( $t = -0.43$ , d.f. = 14,  $P = 0.67$ ), and a linear regression of the pairs of estimates revealed a linear relationship ( $F = 39.10$ , d.f. = 1,13,  $r^2 = 0.75$ ,  $P < 0.0001$ ), with an intercept that did not differ significantly from zero [estimate (SE) =  $-0.023$  (0.043),  $t = -0.55$ ,  $P = 0.59$ ] and a slope that did not differ significantly from one [estimate (SE) =  $1.072$  (0.171),  $t = -0.42$ ,  $P = 0.69$ ]. Thus, estimates based on specimens are repeatable and of a similar magnitude as those obtained using a different filed-based method. Samples from the taxidermist were composed of individuals that had been shot by hunters, killed after collision with windows or cars, or died for other reasons, whereas the mist net samples are likely to be more homogeneous. Despite these differences in cause of inclusion in the two samples, estimates of frequency of fault bars remained consistent.

### RISK OF BREAKAGE OF FEATHERS AT FAULT BARS

Sarasola & Jovani (2006) showed that feather breakage was more likely to occur at wide fault bars. No study has explicitly tested whether feather breakage is more likely to occur at fault bars than expected from random. We compared observed frequency of feather breakage with expected risk of feather breakage by using feathers from 235 prey individuals of goshawks collected in 2006. We measured the width of fault bars to the nearest millimetre, and all had a width of less than 1 mm, which we subsequently used as the maximum width of a fault bar in the subsequent calculations. Next, we measured length of all feathers to the nearest millimetre with a ruler. The observed frequency of feather breakage at fault bars and elsewhere was recorded for all feathers, with breakage being assigned to a fault bar when part of the feather had been broken and a fault bar was clearly visible at exactly the same site. Such breakage always occurred at a fault bar because that is the weakest structural point of a feather, not dissimilar to a line of perforation on a sheet of paper. We estimated expected frequency of breakage at fault bars as the combined width of all fault bars (assuming a width of 1 mm for each fault bar) relative to the total length of all feathers. This value was subsequently multiplied by the number of broken feathers to obtain the expected frequency of feathers broken at fault bars.

Feather breakage more often occurs at the tip of feathers than at the base, perhaps because feather width is greater at the base. If fault bars were distributed nonrandomly along the axis of feathers, this could also affect the distribution of feather breakage. Therefore, in a second analysis, we assumed conservatively that feather breakage only occurred at the distal 25% of the length of feathers and that all fault bars were located in that section. Observed and expected frequency of feather breakage was then re-calculated based on these conservative expectations.

#### FAULT BARS IN PREY AND NONPREY

All wing and tail feathers collected (by J.T.N.) from prey at goshawk nests and their surroundings during three visits to all nests in the study area in Northern Jutland, Denmark, during April to September 2006. Feathers of individual prey were placed in a sealed plastic bag and stored for later investigation of presence and abundance of fault bars. All prey were collected blindly with respect to presence of fault bars and also with respect to information on susceptibility to predation. A total of 235 prey individuals belonging to 23 species were collected. We had no estimate of frequency of fault bars in the general population for three species (*Anas platyrhynchos* L., one individual; *Vanellus vanellus* L., eight individuals; *Corvus monedula* L., four individuals), which were therefore excluded from the analyses. The data are presented in the Supporting information (Appendix S2).

#### ECOLOGICAL VARIABLES

##### *Susceptibility to predation*

An index of prey vulnerability was calculated as observed  $\log_{10}$ -transformed number of prey minus  $\log_{10}$ -transformed expected number of prey, where a value of zero implies that prey were consumed relative to their abundance, a value of +1 implies that prey were consumed ten-fold more frequently than expected from their abundance, and a value of -1 implies consumption ten-fold less frequently than expected. The expected number of prey was estimated from the combined breeding density of all species, the total number of prey items, and the proportion of prey items of each species (for details, see below; see also Møller & Nielsen, 2006).

Nielsen (2004) studied sparrowhawks during 1977–1997 and goshawks during 1977–2004 in an area of 2417 km<sup>2</sup> in Northern Jutland, Denmark. Prey remains of the predators were systematically collected near nest sites during April to September. Collection of prey remains near nest sites ensured that only prey of a given predator were included in

the data set because sparrowhawks and goshawks never bred next to each other (goshawks commonly prey on sparrowhawks). Only prey judged to be less than 1 month old was included in the study because we wanted to be sure that only prey brought by the nest owner was included in the analyses. A total of 31 745 prey items of 66 species of the sparrowhawk and 21 818 prey items of 82 species of the goshawk were used for the present analyses. All nest sites were visited a similar number of times during the breeding season, and sampling effort can therefore be considered to be similar across sites.

We calculated the expected number of prey by using information on density of breeding birds obtained from systematic point counts at randomly located sites in each 5 × 5 km square throughout Denmark (Grell, 1998). Maps of the density of breeding birds are reproduced in Grell (1998) based on systematic point counts of breeding birds carried out by hundreds of amateurs, and the mean density of breeding birds in the study areas of Nielsen (2004: fig. 1) was extracted from these maps. We could only estimate susceptibility indices for species that were breeding locally and hence had estimated breeding densities. Therefore, species with no local breeding populations could not be included in analyses of relationships between fault bars and susceptibility to predation.

##### *Age*

We aged all individuals as yearlings or adults according to age criteria reported by Cramp & Simmons (1977–1994).

##### *Migration distance*

We determined northernmost and southernmost latitude of breeding and wintering distributions, respectively, to the nearest 0.1° for all species for which we estimated frequency of fault bars from Cramp & Simmons (1977–1994). These measures of distribution have previously been shown to provide biologically meaningful measures of distribution (Gaston & Blackburn, 1996). The mean breeding distribution was estimated as the mean of the northernmost and the southernmost latitude of the breeding distribution, and the mean winter distribution as the mean of the northernmost and the southernmost latitude of the winter distribution. We quantified migration distance as the difference in degrees latitude between the mean breeding distribution and the mean winter distribution.

##### *Aerial foraging*

We classified species that relied on flight to obtain food as aerial foragers. Information was mainly obtained from Cramp & Simmons (1977–1994). Thus, birds of prey such as sparrowhawk and kestrel *Falco*



*tinnunculus* L. were classified as aerial foragers, as were swift *Apus apus* L. and sand martin *Riparia riparia* L. Similarly, spotted flycatcher *Muscicapa striata* L., red-backed shrike *Lanius collurio* L., wheatear *Oenanthe oenanthe* L., and willow warbler *Phylloscopus trochilus* L. were scored as aerial foragers. All species were assigned a score of one, whereas all other species were assigned a score of zero.

#### *Sexual dichromatism*

Sexual dichromatism was included as a potentially confounding variable because it was assumed that the intensity of sexual selection could affect ability to produce feathers without fault bars. We used sexual dichromatism rather than the frequency of polygyny, or sexual size dimorphism as an index of intensity of sexual selection, because previous studies have shown that sexual dichromatism captures variance in mating success due to both extra-pair paternity and polygyny (Møller & Birkhead, 1994; Owens & Hartley, 1998; Bennett & Owens, 2002). We scored prey species as sexually monochromatic or dichromatic, using a dichotomous classification with species considered to be monochromatic given a score of zero, if males and females could not be reliably distinguished based on plumage characters according to field guides (Svensson, 1984; Mullarney *et al.*, 2000). Any sex difference in plumage coloration was considered to represent sexual dichromatism, which was scored as one. For example, blue tits *Parus caeruleus* L., which can be reliably sexed based on the intensity of the blue coloration of the crown, were scored as dichromatic, whereas coal tits *Parus ater* L., which cannot be sexed based on plumage characters, were scored as monochromatic. We did not attempt to quantify the magnitude of sex difference in coloration, since we did not know how predators perceive such differences. However, our dichotomous score was strongly positively correlated with quantitative scores from Møller & Birkhead (1994) and Read (1987), suggesting that both dichotomous and continuous scores provide similar information.

#### *Aerial sexual displays*

We classified species as having aerial sexual displays based on Cramp & Simmons (1977–1994). Thus, species with song flight such as skylark *Alauda arvensis* L. and common whitethroat *Sylvia communis* Lath. were classified as having aerial sexual displays, but so were species such as sparrowhawk and barn swallow. All species with aerial displays were given a score of one, whereas all other species were given a score of zero.

#### *Diet*

We classified the amount of animals in the diet, based on Cramp & Simmons (1977–1994), with a score of

zero attributed to species that only consumed plant material, a score of two assigned to species that only consumed animals, and a score of one assigned to species with a mixed diet. This classification was made because a higher frequency of animal proteins may increase frequency of developmental errors during moulting (Murphy *et al.*, 1988).

#### *Body size and body mass*

We recorded tarsus length with a calliper and body mass on a balance directly from the specimens (as delivered to J.E.) that were the basis of this study. None of the specimens used were damaged, and there was thus no reason for expecting body mass to be biased.

The entire data set is provided in the Supporting information (Appendix S3).

### STATISTICAL ANALYSIS

We tested whether the distribution of continuous variables deviated from normality, and appropriate transformations were made to meet requirements for parametric statistical tests. The frequency of individuals with fault bars was square-root arcsine-transformed before analysis, whereas sample size and body mass were  $\log_{10}$ -transformed. Migration distance was  $\log_{10}(x + 1)$ -transformed to account for presence of zeros for resident species. Aerial foraging, aerial sexual display, and sexual dichromatism were dichotomous variables that were treated as dummy variables in the analyses, similar to using a dichotomous variable as a dummy variable in standard regression analyses (Sokal & Rohlf, 1995). These variables were considered to be continuous in the comparative analyses of standardized linear contrasts because intermediate states of the variables were possible and represented biologically meaningful conditions.

We tested for association between age and presence of fault bars by calculating Kendall rank-order correlations between presence of fault bars and age (scored as either yearling or older). The mean correlation coefficient for the different species was, under the null hypothesis, predicted not to differ from zero after  $z$ -transformation, after weighting by sample size because correlation estimates based on larger sample sizes were expected to be more reliable, whereas the alternative hypothesis predicted an overall negative relationship. Similarly, we tested for effects of condition on presence of fault bars by calculating Kendall rank-order partial correlations between presence of fault bars and body mass, after controlling for tarsus length. The mean correlation coefficient for different species was under the null hypothesis predicted not to differ from zero after  $z$ -transformation, and weighting



results obtained based on these branch lengths were compared with those obtained using constant branch lengths (a punctuated model of evolution). None of the results were qualitatively different.

We used multiple regression to find best-fit models with the predictor variables, using JMP (2000). There was no evidence of collinearity between variables as indicated by the maximum correlation between any two variables (Pearson  $r = 0.45$ ). Green (1979) suggests that any correlation less than 0.70 will eliminate serious problems of collinearity.

Regressions based on contrasts were forced through the origin because the comparative analyses assume that there has been no evolutionary change in a character when the predictor variable has not changed (Purvis & Rambaut, 1995).

## RESULTS

### FREQUENCY OF FAULT BARS

The frequency of fault bars varied among species (Fig. 2), with the ancestral state demonstrating a high frequency of fault bars. There was highly significant variation among species in the frequency of fault bars (likelihood-ratio  $\chi^2 = 128.97$ , d.f. = 85,  $P = 0.0015$ ). The mean  $\pm$  SE frequency of fault bars in wing and tail feathers was  $5.9 \pm 0.8\%$  ( $N = 86$  species, range 0–38.5%). Total sample size was 3279 individuals, with a mean  $\pm$  SE of  $34.5 \pm 5.8$  individuals per species. The mean number of fault bars per individual was positively correlated with proportion of individuals with fault bars ( $F = 12.28$ , d.f. = 1,53,  $r^2 = 0.19$ ,  $P < 0.0001$ , slope  $\pm$  SE =  $-2.63 \pm 0.75$ ). This result implies that percentage of individuals with fault bars also reflected abundance of fault bars.

The correlation between presence of fault bars and age (yearlings versus adults) in the sample of species from the taxidermist was in the range  $-0.33$  to  $+0.50$  among 43 species with yearling and adult individuals, with a mean  $\pm$  SE value of  $0.01 \pm 0.03$  (one-sample  $t$ -test based on  $z$ -transformed coefficients:  $t = 0.31$ , d.f. = 42,  $P = 0.76$ ). Only two of 43 correlation coefficients were significant at the 5% level, which was not different from the expected 2.20 cases. Similarly, in the 14 species that were mist-netted [one species (chiffchaff *Phylloscopus collybita* Viell.) was excluded because of complete absence of fault bars], the mean  $\pm$  SE correlation coefficient was  $0.00 \pm 0.02$  (one-sample  $t$ -test based on  $z$ -transformed coefficients:  $t = 0.06$ , d.f. = 13,  $P = 0.95$ ). Thus, there was no evidence of change in the frequency of fault bars from yearlings to adults.

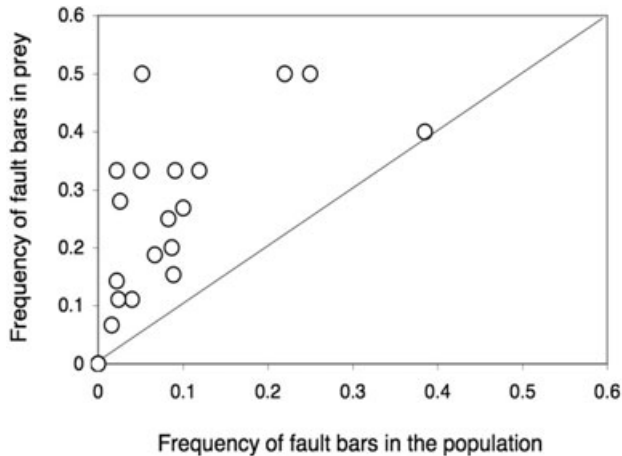
The partial correlation between presence of fault bars and body mass, after inclusion of tarsus length as an additional variable, in the range  $-0.50$  to  $+0.36$

among 47 species with presence of individuals with fault bars, with a mean  $\pm$  SE value of  $-0.02 \pm 0.03$  (one-sample  $t$ -test based on  $z$ -transformed coefficients:  $t = -0.65$ , d.f. = 46,  $P = 0.752$ ). Only two of the 47 correlation coefficients were significant at the 5% level, which was not different from the expected 2.35 cases. Similarly, in 14 species that were mist-netted (chiffchaff was excluded because of complete absence of fault bars), the mean  $\pm$  SE partial correlation coefficient was  $0.00 \pm 0.02$  (one-sample  $t$ -test based on  $z$ -transformed coefficients:  $t = 0.04$ , d.f. = 13,  $P = 0.97$ ). Thus, there was no evidence of change in the frequency of fault bars with condition.

### FREQUENCY OF FAULT BARS AND FEATHER BREAKAGE

Feathers were more likely to break at fault bars than expected by chance. Among 56 individual birds with fault bars out of 235 prey of the goshawk (24%), 16 feathers were broken and, of these 16 broken feathers, 15 (94%) were broken at a fault bar. This gives a frequency of feather breakage of 0.57% ( $N = 2820$ ) of feathers or 27% ( $N = 56$ ) of individuals. The relative distance from the base of the feather to the point of breakage in these 15 feathers was  $0.63 \pm 0.04$  (i.e. the length of feather from base to point of breakage divided by length of total feather estimated as the mean of the two neighbouring feathers). Given that width of a fault bar was less than 1 mm and that tail and wing feathers were on average 13 cm long, the faults bars accounted for much less than 1% of the length of a feather. Therefore, we can conservatively estimate the expected frequency of feather breakage at fault bars from 56 individual birds with fault bars: 156 fault bars recorded in these 56 birds, a total width of 156 mm of all fault bars (156 bars times 1 mm/bar), a length of feathers of 13 cm, and an average of 12 feathers examined for each individual. This gives  $[156 \text{ mm}/(56 \text{ individuals} \times 12 \text{ feathers/individual} \times 130 \text{ mm})] \times 16$  broken feathers, or 0.029 feather breakages at fault bars, if feather breakage was located randomly. This is well below the observed frequency of 15. A  $G$ -test revealed a highly significant difference between observed and expected frequency ( $G = 181.91$ , d.f. = 1,  $P < 0.0001$ ).

If we instead assumed conservatively that feather breakage only occurred at the most distal 25% of feathers, and that fault bars only were located in that section (there were actually equally many fault bars in the proximal and distal 50% of feathers), then expected frequency of feather breakage at fault bars was 0.114, which again is well below the observed frequency of 15, with observations differing significantly from expectations ( $G = 35.22$ , d.f. = 1,  $P < 0.0001$ ).



**Figure 3.** Relative frequency of fault bars in wing and tail feathers of prey of different bird species in relation to the relative frequency of fault bars in wing and tail feathers of individuals from the general populations of different bird species. The line indicates similar frequency of fault bars in prey as in the general population.

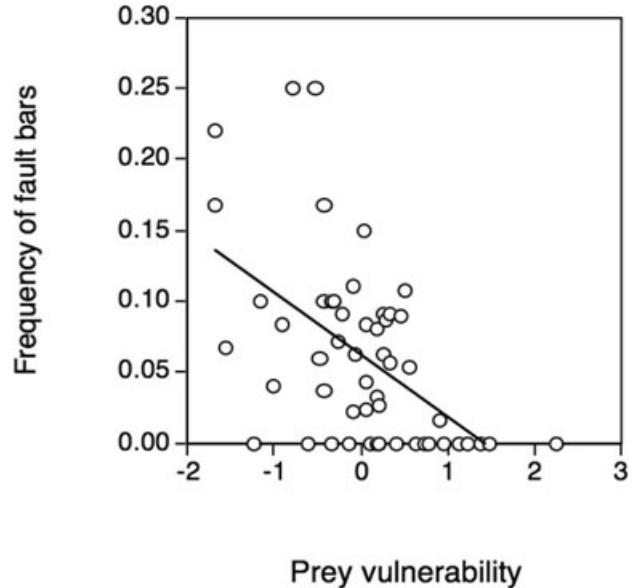
#### FREQUENCY OF FAULT BARS IN PREY AND NONPREY

Mean frequency of fault bars in 20 species with information for the general population and prey revealed a difference of almost a factor three. A total of 23.6% (SE = 2.7) of prey individuals had fault bars, whereas the frequency in the overall population was 8.7% (SE = 2.2), which is a highly significant difference (paired  $t$ -test based on square root-arc-sine-transformed data and weighted by sample size:  $t = 9.11$ , d.f. = 19,  $P < 0.0001$ ; Fig. 3). These differences were also maintained in a paired  $t$ -test of square-root arc-sine-transformed proportion of individuals with fault bars ( $t = -2.90$ , d.f. = 17,  $P = 0.0099$ ). Similarly, proportion of prey individuals with fault bars increased with proportion of all individuals with fault bars (linear regression:  $F = 26.47$ , d.f. = 1, 17,  $r^2 = 0.61$ ,  $P < 0.0001$ , slope  $\pm$  SE =  $0.47 \pm 0.09$ ), with the slope being significantly smaller than one ( $t = 5.90$ , d.f. = 17,  $P < 0.0001$ ), as expected if prey had more fault bars than the general population. Therefore, predation selected against fault bars.

The proportion of adult individuals with fault bars also differed between prey and the population ( $t = 7.20$ , d.f. = 19,  $P < 0.0001$ ; mean  $\pm$  SE for prey:  $23.8 \pm 3.3\%$ ; mean  $\pm$  SE for population:  $8.2 \pm 1.8\%$ ), showing that the difference in the frequency of fault bars was not due to a simple age effect.

#### FREQUENCY OF FAULT BARS AND SUSCEPTIBILITY TO PREDATION

We found a strong negative relationship between susceptibility to sparrowhawk predation and frequency



**Figure 4.** Relative frequency of fault bars in wing and tail feathers of different bird species in relation to susceptibility of species to predation by the sparrowhawk. The line is the linear regression line with the statistics:  $F = 12.84$ , d.f. = 1,51,  $r^2 = 0.20$ ,  $P = 0.0008$ , slope  $\pm$  SE =  $-0.088 \pm 0.024$ .

of fault bars, explaining 20% of the variance (Fig. 4). Across species, the frequency of individuals with fault bars decreased from over 20% to none with an increasing risk of predation by sparrowhawks. The relationship was similar when only based on species with at least some fault bars, thus excluding species with zero fault bars ( $F = 6.43$ , d.f. = 1,33,  $r^2 = 0.16$ ,  $P = 0.016$ , slope  $\pm$  SE =  $-0.055 \pm 0.022$ ). A regression weighted by sample size gave a qualitatively similar conclusion as the unweighted regression ( $F = 8.85$ , d.f. = 1,51,  $r^2 = 0.15$ ,  $P = 0.0045$ , slope  $\pm$  SE =  $-0.074 \pm 0.025$ ). Finally, the conclusion was similar when calculations were based on standardized linear contrasts rather than species-specific values (Table 1). Analyses based on mean frequency rather than prevalence of fault bars produced similar conclusions. For example, susceptibility to predation by the sparrowhawk was significantly negatively related to mean frequency of fault bars among species ( $F = 5.03$ , d.f. = 1,50,  $r^2 = 0.09$ ,  $P = 0.029$ , slope  $\pm$  SE =  $-5.252 \pm 2.342$ ).

Susceptibility to predation by the goshawk was independently related to frequency of fault bars ( $F = 7.02$ , d.f. = 1,55,  $r^2 = 0.11$ ,  $P = 0.011$ , slope  $\pm$  SE =  $-0.027 \pm 0.010$ ). A multiple regression analysis revealed independent effects of susceptibility to predation by both predators on frequency of fault bars ( $F = 5.85$ , d.f. = 2,34,  $r^2 = 0.26$ ,  $P = 0.007$ , slope  $\pm$  SE



**Table 1.** Multiple linear regressions with prevalence or frequency of fault bars (dependent variables) and prey susceptibility and confounding variables (independent variables)

Variable	Sum of squares	<i>F</i>	<i>P</i>	Slope ± SE
<b>Prevalence of fault bars</b>				
Species				
Sparrowhawk prey susceptibility	0.341	19.68	< 0.0001	-0.113 ± 0.025
Migration distance	0.063	3.61	0.064	-0.052 ± 0.027
Contrasts				
Sparrowhawk prey susceptibility	0.028	7.18	0.012	-0.086 ± 0.032
Body mass	0.014	3.59	0.068	-0.181 ± 0.096
Migration distance	0.025	6.47	0.016	-0.108 ± 0.043
<b>Frequency of fault bars</b>				
Species				
Sparrowhawk prey susceptibility	0.012	13.96	0.0005	-0.021 ± 0.006
Migration distance	0.005	6.16	0.017	-0.015 ± 0.006
Contrasts				
Sparrowhawk prey susceptibility	0.0009	5.61	0.024	-0.015 ± 0.006
Migration distance	0.002	13.40	0.0009	-0.037 ± 0.010
Aerial foraging	0.0009	5.60	0.024	0.027 (0.011)

For further details, see Material and methods. The statistics for the models were for (A)  $F = 11.44$ , d.f. = 2,47,  $r^2 = 0.33$ ,  $P < 0.0001$ , (B)  $F = 4.46$ , d.f. = 3,31,  $r^2 = 0.30$ ,  $P < 0.010$ , (C)  $F = 9.68$ , d.f. = 2,46,  $r^2 = 0.30$ ,  $P = 0.0003$ , and (D)  $F = 6.58$ , d.f. = 3,31,  $r^2 = 0.39$ ,  $P = 0.0014$ .

for sparrowhawk =  $-0.082 \pm 0.03$ ,  $t = -2.50$ ,  $P = 0.017$ ; slope ± SE for goshawk =  $-0.027 \pm 0.13$ ,  $t = -2.08$ ,  $P = 0.046$ ). The two indices of susceptibility to predation were not significantly correlated (based on information on prey vulnerability index for 41 species of prey that were common to the two predators:  $F = 1.29$ , d.f. = 40,41,  $P = 0.21$ ).

A multiple regression for prevalence of fault bars revealed a significant effect of prey vulnerability for sparrowhawk and migration distance (Table 1). In an analysis of contrasts, there was similar significant effects of susceptibility to sparrowhawk predation and migration distance, with no additional significant effect of aerial display, sexual dichromatism, diet, aerial foraging, or body mass (Table 1). An analysis with mean frequency of fault bars as the dependent variable showed that both susceptibility to sparrowhawk predation and migration distance were significant predictors (Table 1). An analysis of standardized linear contrasts revealed significant effects for susceptibility to predation by sparrowhawk, with additional effects of migration distance and aerial foraging (Table 1).

## DISCUSSION

The main findings of our comparative analyses were the significant differences in the frequency of fault bars among species, with the ancestral state having a high frequency of fault bars. Age and condition were

not related to the frequency of fault bars within species. Wing and tail feathers were more likely to break at fault bars than expected by chance. Prey of goshawk had a three-fold greater frequency of fault bars in their feathers than expected for the general population. Finally, the interspecific variation in the frequency of fault bars was explained by differences in susceptibility to sparrowhawk predation, migration distance, and aerial foraging. Species more susceptible to predation had lower frequencies of fault bars in their plumage than the average species.

We hypothesized that fault bars arise due to the lack of developmental control or differences in susceptibility to stress during moulting. Transparent fault bars develop due to errors during ontogeny (Michener & Michener, 1938; Wood, 1950; Jovani & Blas, 2004), and previous studies have hypothesized that feathers commonly break at this point because a lack of keratin weakens the feather (Kose *et al.*, 1999; Dawson *et al.*, 2001). We explicitly tested this prediction by comparing observed frequency of feather breakage at fault bars with the null expectation of random breakage along the shaft, demonstrating an elevated risk of feather breakage at fault bars.

There were significant interspecific variation in frequency of fault bars among birds. We tested whether fault bars simply reflected underlying condition. However, across 47 species of birds delivered to J.E., the average partial correlation between the presence of fault bars and body condition was  $-0.02$  (not dif-

fering significantly from zero) and a similar conclusion was reached for a sample of 14 species of mist-netted birds. This provides evidence of consistency in the conclusions suggesting that this could not be attributed to the effects of biased samples. Because young birds have been exposed to less intense natural selection than adults, we might expect fault bars to be more common in young individuals. However, the average correlation coefficient between presence of fault bars and age was +0.01 in 43 species delivered to J.E. and +0.00 in 14 species mist-netted by A.P.M. (not significantly different from zero). Previous studies of condition in birds, using the same measure as that adopted in the present study, showed that individuals in better condition reproduce earlier and lay more eggs than individuals in poor condition (Merilä, Przybylo & Sheldon, 1999; Kruuk, Merilä & Sheldon, 2001). In addition, the measure of condition adopted in the present study has a quantitative genetic basis (Smith & Westermarck, 1995; Merilä, 1996; Merilä *et al.*, 1999). Therefore, fault bars do not simply reflect poor body condition in the traditional sense of the term.

The most important finding of the present study was a greater frequency of fault bars in prey of the goshawk than in the general population. In terms of intensity of natural selection, the mean difference in phenotype between prey and the general population amounted to: [0.494 (mean square root arcsine-transformed frequency of fault bars in prey) – 0.221 (mean square root arcsine-transformed frequency of fault bars in the population)]/0.683 (standard deviation of square root arcsine-transformed frequency of fault bars in the population), or 0.4 standard deviations, which is strong compared to published estimates of directional natural selection (Kingsolver *et al.*, 2001).

The ancestral state of fault bars was a high frequency and interspecific differences in frequency must have evolved due to reductions in frequency. Such reductions have evolved repeatedly due to differences in intensity of natural selection, as reflected by the prey susceptibility index for sparrowhawk and goshawk, but also to migration distance and perhaps aerial foraging, with the latter result only appearing in one of four analyses (Table 1). When natural selection was intense, as in species that attract particular attention from agile predators, we found a dramatic decrease in frequency of fault bars. This suggests that fault bars are particularly costly during predation attempts. Interestingly, predators may themselves affect the development of fault bars. Starlings (*Sturnus vulgaris* L.) that moulted in absence of cover from predators, and hence were unable to take refuge when exposed to predation risk, developed more fault bars than starlings with access to cover (Witter & Lee, 1995: 306).

The two predators independently selected against presence of fault bars because the prey of the goshawk differed from the general population in frequency of fault bars, and because the two indices of susceptibility to predation both predicted the frequency of fault bars. The relationships between the frequency of fault bars and susceptibility to two species of predators were not confounded by the population density of prey (Møller & Nielsen, 2006) or several other potentially confounding variables. Sparrowhawk and goshawk are the most common predators of birds throughout large parts of the Palearctic region, accounting for a large fraction of the total impact of predation on birds.

Other causes of natural selection explained additional interspecific variation in frequency of fault bars. Consistently, both the prevalence and frequency of fault bars across species decreased with migration distance, as expected because of extreme costs of migration (Berthold, 2001). In analyses of contrasts for the frequency of fault bars, we found a weak positive relationship between fault bars and aerial foraging (Table 1), contrary to the predicted negative association. This result may have arisen from chance alone, or it may reflect the fact that aerial foragers generally are very good fliers with superior ability to escape avian predators, thus partly eliminating predation costs of fault bars.

In conclusion, the frequency of fault bars varied among species, and costs of natural selection in terms of susceptibility to predation and long distance migration, reduced such errors, indicating that developmental control or susceptibility to stress can change when intensity of natural selection changes.

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## SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

**Appendix S1.** Frequency of fault bars among individuals of 15 species of birds obtained for the present study and from field samples of birds captured in mist nets.

**Appendix S2.** Frequency of fault bars in prey of the goshawk and among individuals from the general population.

**Appendix S3.** Information on frequency of fault bars, mean number of fault bars, sample size, susceptibility to predation by the two predators and the number of prey individuals, migration distance (degrees latitude), aerial foraging (0, absent; 1, present), aerial sexual display (0, absent; 1, present), sexual dichromatism (0, monochromatic; 1, dichromatic), body mass (g) and diet (0, plants; 1, mixed; 2, animals) of the different species.

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