

Risk of feather damage explains fault bar occurrence in a migrant hawk, the Swainson's hawk *Buteo swainsoni*

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Fault bars are common stress-induced feather abnormalities that could produce feather damage thus reducing flight performance. For that reason, it has been hypothesized that birds may have evolved adaptive strategies that reduce the costs of fault bars (the 'fault bar allocation hypothesis'). An untested prediction of this hypothesis is that fault bars in important feathers for flight (wing and tail) should be less abundant where they produce more feather damage. We tested such a prediction using moulted wing and tail feathers of the long-distance migrant Swainson's hawk *Buteo swainsoni* in its Argentinean wintering quarters. We recorded the occurrence of fault bars of different strengths (light, medium and strong) and the damage (lost of a portion of the vane) produced by them. The occurrence of fault bars was very variable, with strong ones being rare throughout and light and medium fault bars being more frequent in the tail than in the wing. Risk of feather damage was similarly high and low across feather groups for strong and light fault bars, respectively, and higher in the wing than in the tail for medium strength. The occurrence of fault bars of different strengths on different feather groups was negatively correlated with their propensity to produce feather damage. At low damage risk (B5%), the occurrence of fault bars was highly variable depending on the feather group, but above 5% of feather damage the occurrence of fault bars was highly reduced throughout. Our results supports the 'fault bar allocation hypothesis' of natural selection reducing fault bar occurrence where fault bars are more risky, but further suggest that selection pressure could be relaxed in other instances, leaving the way free for other mechanisms to shape fault bar occurrence.

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Fault bars are common abnormalities in birds' feathers (Riddle 1908), that look like narrow and translucent bands arranged approximately perpendicular to the feather rachis. They are produced by some barbules being slimmer or completely absent as a result of a variable time lag on the deposition of keratin during feather grow (Murphy et al. 1989, Prum and Williamson 2001). Although mechanisms promoting fault bars are still poorly understood, nutritional conditions (Slagsvold 1982, Machmer et al. 1992) and stress episodes (i.e. escape from predators; King and Murphy 1984, Negro et al. 1994) are some of the most commonly evocated causes for fault bar formation.

Irrespective of the mechanisms promoting fault bars, they could produce potential flight costs because of partial feather damage or even complete feather breakage (Slagsvold 1982, Machmer et al. 1992). Contrary to feathers lost during moult, which are immediately replaced by new ones, damaged or broken feathers are not replaced until the next normal moult of the plumage. Thus, feather damage resulting from fault bars may reduce wing-tail surface area for long time periods. All of this is relevant for bird fitness because wing load (body weight/wing area) is crucial for flight performance (Pennycuik 1989), birds being forced to reduce their weight during even slight reductions of wing area

(Swaddle and Witter 1997, Lind and Jakobson 2001, Senar et al. 2002). Moreover, experimental reductions of wing area are known to increase the energetic demands of birds, lowering their reproductive success (Mauck and Grubb 1995, Velando 2002). Similarly, sharp loses of tail area have been reported to compromise manoeuvrability during flight (Fisher 1959, Mueller et al. 1981).

Jovani and Blas (2004) proposed that birds should have evolved adaptive strategies for reducing the costs of fault bars ('fault bar allocation hypothesis'). For important flight feathers such as wing and tail feathers, an untested prediction of this hypothesis is that the occurrence of fault bars should be lowest in those feathers where the risk of feather damage due to fault bars is highest. In other words, different probability of feather damage by fault bars in important flight feathers should be behind the observed variability in fault bar occurrence among feathers (e.g. King and Murphy 1984, Machmer et al. 1992, Serrano and Jovani 2005). An indirect evidence of it was found studying feathers growing simultaneously in white stork *Ciconia ciconia* chicks, where fault bars were found to be less abundant on those feathers thought to have more strength requirements during flight, and thus possibly a higher probability of feather damaging due to fault bars (Jovani and Blas 2004). However, a direct test of this prediction is lacking.

The Swainson's hawk *Buteo swainsoni* breeds in North America and spends the boreal winter in southern South America, mainly in the central provinces of Argentina (England et al. 1997), performing a migratory trip of ca. 10,000 km each way (Fuller et al. 1998). During migration they mainly perform soaring flight benefiting from thermals (Smith 1980). Soaring flight has low energy demands, but imposes a high flexion stress on the distal primary feathers that curve up for reducing the air drag (Cone 1962, Tucker 1993). Moreover, they show diverse flight foraging displays, ranging from hunting small vertebrates by direct flight, hovering or perching (England et al. 1997), to preying upon invertebrates captured in the air while soaring in thermals (Jaramillo 1993, Rudolph and Fisher 1993, Sarasola and Negro 2005). In that way, a feather damage due to a fault bar could impose an important flight constrain. Although most detailed data exists on the timing of moult of Swainson's hawks for the breeding season (Schmutz 1992), hawks also moult during the wintering season in Argentina (Goldstein et al. 1999, Bechard and Weiden-saul 2005). Both the high flight requirements and moult features thus make the Swainson's hawk an interesting study model for the analysis of the adaptive nature of fault bar distribution patterns in birds. Moreover, by studying moulted feathers we benefited from a more similar age of each feather studied, and thus our results had not the bias of different ages of feathers as could happen when studying feathers on wild-caught birds. In

any case, the age of feather has been found not correlated with feather damage due to fault bars in a study with cranes (Jovani et al. unpubl. data).

Here, we tested the prediction of the "fault bar allocation hypothesis" by studying the occurrence of fault bars, the propensity of fault bars producing feather damage, and the correlation between both variables in the Swainson's hawk. Occurrence is used throughout to resume in a same word both prevalence (i.e., percentage of feathers with fault bars) and abundance (i.e., number of fault bars). The role of the tail in flight performance refers to stability, balance, and turning (Thomas 1996a,b), so the intensity of the induced drag supported by tail feathers is expected to be lower than that of outer wing feathers involved in flying activities like soaring. Within the wing, flight requirements are lower in the innermost than in the outermost wing feathers, especially for gliding (Tucker 1991). Thus, according to the 'fault bar allocation hypothesis', we expected that: 1) fault bars occurrence in the Swainson's hawk should be lower on wing than on tail feathers and within the wing lower in distal than in proximal feathers, 2) the risk of feather damage due to fault bars must be lower in the group of feathers with lower flight requirements (e.g., the tail) than those supporting more physical stress during the flight such as the distal wing feathers, and 3) a negative relationship between risk of feather damage and prevalence and abundance of fault bars.

Methods

Feather collection and analyses

Swainson's hawks are territorial during the breeding season, but they became gregarious in the winter quarters where they roost and hunt in flocks of hundreds or even thousands (England et al. 1997). We benefited from these large aggregations collecting 801 moulted feathers from 2001 to 2003 from the ground of 12 different roosts in central Argentina (La Pampa, Córdoba and Buenos Aires provinces).

In the laboratory, we used a museum reference skin to classify wing feathers in three groups: Pdist (distal primaries): from the outermost to the sixth primary (N=124 feathers), Pprox (proximal primaries): primaries fifth to first (N=101 feathers), and S-T: secondary and tertial feathers (N=289 feathers). Primary feathers were separated in two groups because their distinct morphology (distal ones being more asymmetric) and function during flight (see above). We did a unique group with secondaries and tertials because the small number of possible tertials collected and because they show a gradual change on morphology from outer secondaries to inner tertials, being difficult to differentiate. Tail feathers were classified in three groups also considering their distinct morphology: Rdist (distal

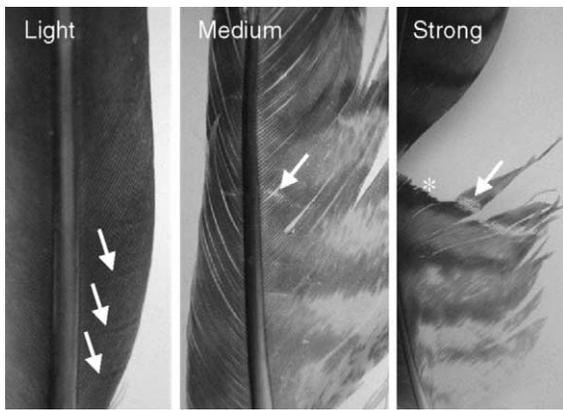


Fig. 1. A gradient of fault bar strengths found on the studied feathers. Arrows indicate fault bars. The asterisk indicates a break of feather barbules because of a strong fault bar.

rectrices): the external and more asymmetric feathers of the tail (N=41 feathers), Rprox (proximal rectrices): internal rectrices (from rectrices two to five; N=204 feathers), and Rcen (central rectrices): the more symmetric, central pair of tail feathers (N=42 feathers).

Each feather was inspected for the presence of fault bars by changing the angle of light incidence and also holding the feathers against the sky. We categorized each fault bar as light (absence of some barbules producing a visible discontinuity on the structure of the feather; N=407), medium (a narrow, i.e. 1 mm, translucent line across the feather N=254), or strong (1 mm, translucent line across the feather N=63; see Fig. 1 for examples, and Fig. 3 for sample sizes detailed for each feather group). In extreme instances, fault bars produced the cut of a portion of the vane from its position up to the distal edge of the feather (Fig. 1). We recorded whether or not each fault bar produced breaking of feather barbules.

We calculated the prevalence and abundance for fault bars and the risk of feather damage due to fault bars. Prevalence of fault bars was calculated as the percentage of feathers that have fault bars, while abundance of fault bars was calculated as the mean number of fault bars

found on each feather. We estimated the risk of feather damage due to fault bars as the ratio between the number of fault bars producing feather damage and the total number of fault bars. All these parameters were estimated for each of the feather groups and fault bar categories.

We also calculated the prevalence and abundance of feather damage due to fault bars and looked for differences between feather groups. Prevalence of feather damage was the percentage of feathers with damage due to fault bars while abundance of feather damage was estimated as the number of fault bars on each feather producing feather damage.

The use of moulted feathers precluded us to do within bird comparisons of the occurrence of fault bars in different feathers. Rather, we included in the same analyses feathers from different birds. This is a potential source of noise because feathers from individuals with different age, sex, and history are grouped. However, for species such as raptors, a given individual uses to have different feather generations, and thus feathers grown at different time and of different age. In this way, using moulted feathers in our study case is a good alternative that allow the study of a large sample size, while being studying feathers of similar age (all are recently moulted feathers).

Because the non-parametric nature of the studied variables (percentages, and counts greatly right skewed) we used Chi-square, Mann-Whitney and Kruskal-Wallis two-tailed tests.

Results

Prevalence and abundance of fault bars

The prevalence of light fault bars was higher on tail than on wing feathers, and variable within wing feathers (Table 1; Fig. 2a). The prevalence of medium fault bars was also variable, higher on the tail than on the wing, and variable within tail feathers (Table 1; Fig. 2a). However, strong fault bars occurred at a low prevalence throughout and we did not find differences among

Table 1. Differences in fault bar prevalence and abundance for wing and tail groups of feathers. Chi-square (P-value) for prevalence, and Kruskal Wallis (for >2 groups) and U Mann-Whitney (for two groups) for abundance comparisons are shown. We did not find differences in the prevalence and abundance of strong fault bars among feather groups (see text).

	df	Fault bar strength	
		Light	Medium
Prevalence			
Wing vs. tail	1	36.84 (B0.0001)	12.70 (B0.001)
Within the wing	2	6.25 (0.04)	4.31 (0.11)
Within the tail	2	3.43 (0.17)	13.10 (B0.01)
Abundance			
Wing vs. tail	1	60208 (B0.0001)	66459 (B0.0001)
Within the wing	2	7.41 (0.02)	3.86 (0.14)
Within the tail	2	3.67 (0.15)	12.88 (B0.01)

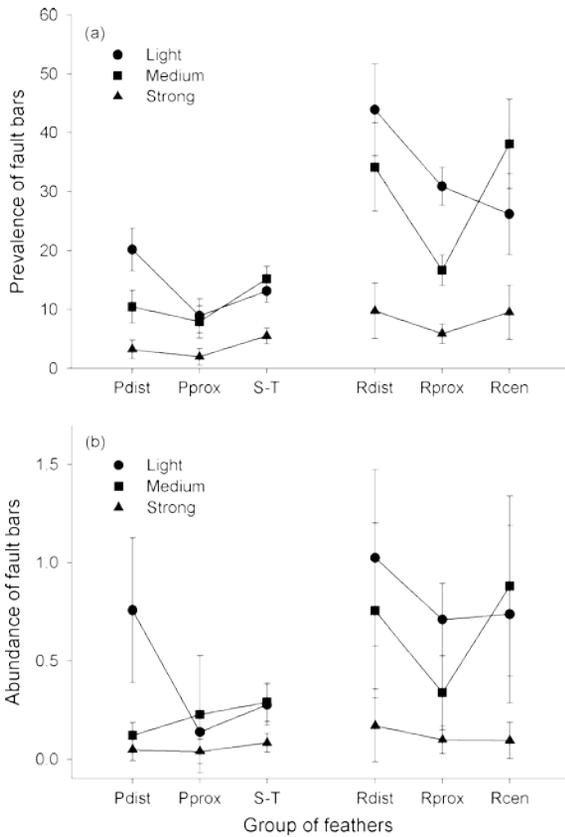


Fig. 2. (a) Prevalence (% of feathers with fault bars), and (b) abundance (mean 95% CI of number of fault bars per feather) according to feather group.

feather groups ($\chi^2=6.63$, $P=0.25$; Fig. 2a). For the abundance of light and medium fault bars we found a similar picture than for prevalence (Table 1, Fig. 2b), and the number of strong fault bars was evenly distributed (Kruskal Wallis $\chi^2=6.56$, $P=0.26$; Fig. 2b).

Risk of damage according to fault bar strength and feather group

The probability of a fault bar producing the breaking of feather barbules was greatly dependent on fault bar strength ($\chi^2=78.26$, $P<0.001$), increasing from light (two breakings out of 407 fault bars; 0.5%), to medium (22/254; 8.7%), and strong fault bars (17/63; 27.0%).

Light fault bars constituted a low risk of breaking of barbules in all feather groups ($\chi^2=1.93$, $P=0.86$), and strong fault bars represented a higher and similar risk of breaking throughout ($\chi^2=1.19$, $P=0.95$; Fig. 3). However, fault bars of medium intensity differed on their propensity of breaking of feather barbules ($\chi^2=28.22$, $P<0.001$), being higher on the wing than on the tail feathers ($\chi^2=14.79$, $P<0.001$), differing among

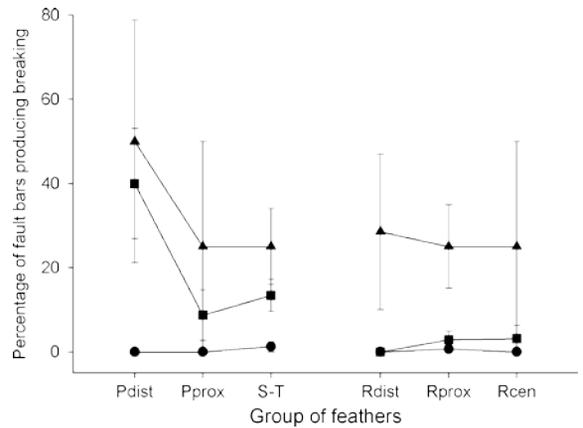


Fig. 3. Percentage (% of fault bars producing feather damage). Samples sizes (number of fault bars) for feather groups from left to right were: Light: 94, 14, 81, 42, 145, and 31; Medium: 15, 23, 82, 32, 70, and 32; Strong: 4, 4, 24, 7, 20, and 4.

wing ($\chi^2=7.81$, $P=0.02$), but not among tail feathers ($\chi^2=0.97$, $P=0.62$; see Fig. 3).

Fault bar prevalence and abundance in relation to the risk of damage

The risk of feather damage due to fault bars was negatively correlated with the prevalence (Spearman $r=-0.68$, $N=18$, $P<0.01$) and the abundance (Spearman $r=-0.77$, $N=18$, $P<0.001$) of fault bars among feather groups (Fig. 4). At a low risk of breaking of feather barbules (5%) fault bars occurred at a variable prevalence and abundance, but when the risk of breaking exceeded the 5%, the occurrence of fault bars was always reduced at low levels for all feather groups and fault bar strengths (Fig. 4).

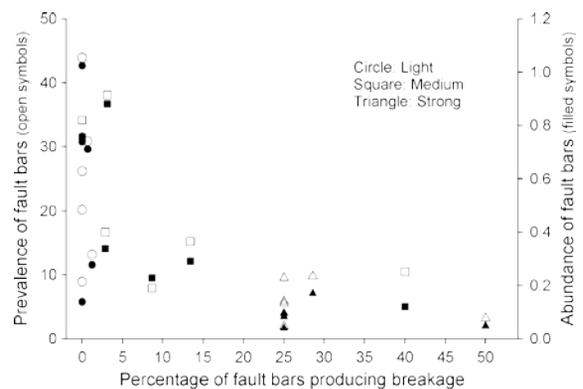


Fig. 4. Relationship between prevalence of fault bars producing breaking of barbules (risk of feather damage due to fault bars) and prevalence (% of feathers with fault bars) and abundance (mean 95% CI of number of fault bars per feather) of fault bars.

Prevalence and abundance of feather damage

The percentage of feathers with at least one break on their barbules was similarly low (between 3 and 6%) across feather groups ($\chi^2_5=1.45$, $P=0.92$; Fig. 5). The abundance of such breaks was also equally low (between 0.030 and 0.065 breaks per feather) among feather groups (Kruskal-Wallis $\chi^2_5=1.46$, $P=0.92$; Fig. 5).

Discussion

Ours is the first study linking the occurrence of fault bars and the damage they produce on the feathers of birds. Three main results may be noted: (a) light fault bars almost never produced feather damage in any group of feathers, (b) strong fault bars constituted a similar high risk of feather damage throughout, and (c) medium fault bars showed a variable risk of feather damage, from being as risky as strong fault bars on distal primary feathers, decreasing on proximal wing feathers, to being as innocuous as light fault bars on the tail. These results support the higher strength requirements of wing vs. tail, and in some cases that of distal vs. proximal wing feathers supposed in previous tests of the 'fault bar allocation hypothesis' (Jovani and Blas 2004, Serrano and Jovani 2005). However, they also reveal the irregular pattern for the prevalence and abundance of fault bars through different feather and fault bar categories. For example, prevalence and abundance of light fault bars was higher in the most distal wing feathers while medium fault bars were evenly distributed in the wing with similar fault bar abundances among wing feathers. Such results hence do not completely support our prediction of lower prevalence and abundance of fault bars in those feathers with highest flying requirements, and suggest that more work is needed here.

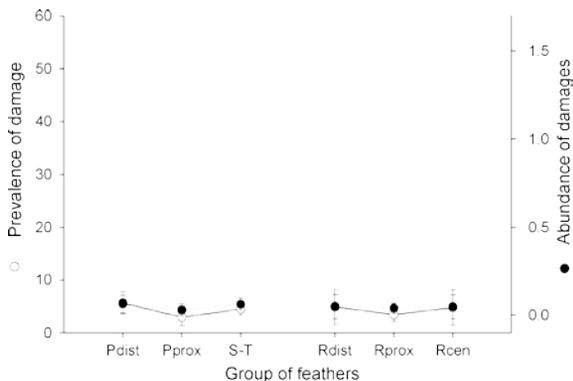


Fig. 5. Prevalence (% \pm SD of feathers with fault bars) and abundance (mean \pm 95% CI of number of fault bars per feather) of feather damage by fault bars along wing and tail feathers. Note the same scale than Fig. 2 for comparison.

Medium fault bars were more risky in the most distal wing feathers when compared with inner wing and tail feathers. However, light fault bars were inoffensive in all feather tracts, while strong fault bars showed a high risk of feather damage through.

The relationship between the pattern of prevalence and abundance of fault bars was in accordance with their riskiness. That is, at a low risk of feather damage (B5%: light fault bars throughout, and medium fault bars on the tail) the occurrence of fault bars was highly variable, but above a 5% threshold (strong fault bars throughout, and medium fault bars on the wing) the occurrence of fault bars was low in all cases. Thus, more or less innocuous fault bars were highly variable on their occurrence, but risky fault bars never reached the high occurrence of unrisky fault bars in any group of feathers. This could easily explain why the occurrence of feathers with some damage by fault bars was very low, and similar, among group feathers.

It is curious how despite all the previous results match only partially with our initial predictions, the relationship between fault bar occurrence and fault bar risk of damage was so clear (Fig. 4). We envision two important factors to explain this pattern. First, a horizontal ordering because of simple physical reasons with light fault bars mainly on the left, medium in the centre and strong ones at the right. Second, a vertical distribution shaped by natural selection that tend to minimize in general those fault bars that produce more feather damage, that is, medium and strong ones. However, light fault bars were not so shaped by natural selection, and greatly differed among feather groups. Note moreover, the interesting deviations of some points from this general pattern. For instance, there was a vertical shift of two points of medium strength fault bars, that occurred at the same level that the more frequent light fault bars, but accordingly, they were also low risky as the rest of light fault bars.

In this way, the similar low occurrence of strong fault bars across feather groups, and the higher occurrence of medium fault bars on the tail than on the wing feathers could be explained by the damage probability of these fault bars upon feathers. Accordingly, fault bars have been found to be more prevalent on the tail than on the wing feathers for other three Buteo species, but a similar occurrence between the tail and the wing was found in the same study for an owl species (*Strix varia*, Hawfield 1986). The prevalence of fault bars has been also found to be lower in the wing than on the tail feathers of other raptor species such as the American kestrel *Falco sparverius* (Negro et al. 1994, Bortolotti et al. 2002) and the osprey *Pandion haliaetus* (Machmer et al. 1992), and passerine species such as the white-crowned sparrow *Zonotrichia leucophrys* (King and Murphy 1984) and the Barn Swallow *Hirundo rustica* (Serrano and Jovani 2005). On the contrary, fault bars are common and

equally abundant on wing and body feathers of the non-flying ostriches *Struthio camelus* (Duerden 1909). This suggests that the flight style and morphology of the species could greatly shape the risk of feather damage by fault bars, and thus its occurrence pattern across feather groups, being an issue that requires further comparative studies (Serrano and Jovani 2005).

The low riskiness of light fault bars throughout wing-tail feathers could not explain, however, why they were more common in the tail than on the wing feathers. It is thought that fault bars are produced by the contraction of the musculature around the feather follicle during feather formation (Murphy et al. 1989). For lowering (or even precluding its formation) the strength of fault bars, natural selection could have thus operated through mechanisms aimed to reduce the contraction strength of the musculature during stressful episodes. Therefore, feather follicle wing musculature in the study species would be more relaxed than on the tail during a stress episode because of the risk of producing fault bars of medium and strong strength. This physiological inertia could be an explanation of why light fault bars were also more common on the tail than on the wing feathers.

The results presented here, together with previous indirect evidence reported elsewhere, suggest that the probability of formation of fault bars is lowered in an adaptive way in those feathers with more strength requirements during flight, according to the 'fault bar allocation hypothesis' (Jovani and Blas 2004). However, the fingerprint of the natural selection could not be found in those feathers where fault bars are more inoffensive, leaving the way free for other mechanisms to operate. Further studies of the external factors and the physiological mechanisms that produce fault bars of different strengths are needed to reach a deeper understanding of the power of the 'fault bar allocation hypothesis' to explain fault bar occurrence, and its intimate relationship with the evolutionary history of bird flight.

Acknowledgements – We wish to thank to M. Santillán, M. Galmes, V. Salvador, M. Reyes, A. Travaini and J. J. Negro for help collecting feathers. We thank A. Lanusse, S. Salva, M. Alliaga, J. Montoya and local landowners for their hospitality and logistic support during fieldwork in Argentina. D. Serrano and E. Ursúa made useful suggestions to a previous draft of this manuscript. We also appreciate the suggestions and comments made by Johan Lind and one anonymous reviewer that greatly improved this manuscript. This study was supported by a grant from the Wildlife Conservation Society (USA). While doing this research, JHS was supported by a scholarship from Consejo Nacional de Investigaciones Científicas y Técnicas de Argentina (CONICET) and RJ was supported by a grant from Telefónica Móviles S.A.

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(Received 27 April 2005, revised 7 September 2005, accepted 13 September 2005.)