Fault bars - a review

by

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In another article on my web site I have written about feathers in Danish, "Fjer, et af naturens mesterværker", free translated: feathers sit atop a pinnacle of evolutionary success, and here is fault bars only very superficially dealt with. As an example of how exciting feathers are, and how many different opportunities for research they offer, I have tried in the following to dig a spit deeper, however, without being too technical. I have described the fault bars a little more in detail, but first of all explained what cost it entails for the individual bird and, still more interestingly I have demonstrated how natural selection does not always produce the most perfect result as many believe. To that end I have studied all written about fault bars I have found and also added a little of my own experience.

Fault bars are translucent bands or more rarely spots in feathers, produced by stressful and adverse conditions during feather formation and caused by defective barbule formation, and they are often points of feather breakage It has been widely assumed that fault bars result from malnutrition during the period of feather growth. However, new investigations have shown that the release of this phenomenon is due to a complex of stress factors where hunger only count for a little part. Important among these are the ones that directly influence the normal course of life and affect metabolism, e.g. handling, either in measuring and weighting a bird or for ringing purposes, and captive birds are known to develop more fault bars than wild birds, e.g. in aviaries without cover, but also other anthropogenic disturbances like, e.g. noise from traffic. So may short- or long-term adverse and unpredictable changes in environment conditions like bad weather. The frequency of fault bars varies from family to family, crows have many, swifts few and nestlings more than adults.

Birds with many fault bars have a lower probability of survival and less success in finding a mate, because the absence of fault bars is a sign of superior quality (good genes or good quality), and some birds are more stress tolerant than others. Because the occurrence of fault bars is a fault development which is a great handicap for the bird, the forces of natural selection have operated on this trait: Birds with a high risk of predation have therefore fewer fault bars than those rarely preyed upon, and the frequency is higher in tail- than in flight feathers and more abundant in tertials than in primaries, long known as feathers less important for flight performance.

The most common abnormality in feathers is fault bars. How often they occur is shown by a new study, in which 3.279 passerine bird skins were examined and 5.9% showed one or more fault bars in their flight- and tail feathers (Møller et al. in prep.) but some species have more often fault bars than others, e.g. among 1919 American Kestrels (*Falco sparverius*) it was even 91.5% (Bortolotti et al. 2002) Therefore it is surprising that so little has been written about this phenomenon, its causes and costs, and the few works written are often found in obscure periodicals. If we turn to the large handbooks, we find that fault bars get ten lines by Campbell and Lack (1985, p. 474) and 11 lines by Terres (1980, p.548). In the new *Handbook of Bird Biology* from Cornell Lab in USA it is only indirectly mentioned on page 3:28: "nutritional deficiencies can lead to minor changes in barbule structure", and that in spite of the fact that the handbook is a giant of more than 1,300 pages (Podulka et al. 2004). In other handbooks like van Tyne and Berger (1976), Brooke and Birkhead (1991) and Gill (2003) fault bars are not mentioned at all, and even Lucas and Stettenheim (1972) do not mention them. These few examples must be sufficient to demonstrate how little attention these bars have got until now. Because fault bars have great significance for the well-being of the birds, and in some cases even for their survival, it must be of interest to know more about them, not less for ringers, aviculturists and others who study birds, and most of all of concern for conservationists. The following give an up-to-date review of our knowledge, what it means for the individual bird, and maybe most fascinatingly, how natural selection has changed the frequency of this obvious error in the development of feathers.

How to recognise a fault bar

The first to describe this phenomenon was Riddle in 1908. He described fault bars as being approx. one mm or less wide, translucent cross stripes where during the growth of the feather a disturbance has taken place. They occur either on the inner- or outer vane and in some cases across both vanes. The angle of the stripe to the feather shaft deviates a little from 90^{o}, but the stripe never runs parallel to the feather barbs. (Illustr. 1)

A microscopic enlargement of a fault bar shows how the individual barbs are bent due to the defective structure of the barbules and the hooks, and the barbs are also thinner at the place in question (Illustr. 2). A rarer variant of a fault bar is a spot in the feather instead of stripes (Murphy et al. 1989) (Illustr. 3) The damage to the structure that the fault bars bring about often causes the barbs or the whole web with the shaft to break off. (Illustr. 4). In extreme cases this can lead to the bird becoming flightless (Stiefel 1985). Among 235 prey of the Northern Goshawk (*Accipiter gentiles*) 16 feathers were broken, and of these 15 were broken at a fault bar (Møller et al. in prep.). Fault bars can occur everywhere in the plumage, yet the frequency varies even within each bird family, sex and age-group (Møller 1994).

Illustr.1. A distinctive fault bar from a Jay's (*Garrulous glandarius*) tail feathers.
Photo: Wolf Dieter Busching.

Illustr. 2. Microscopic entlargemnet of a fault bar 80 X entlarged. From Stiefel (1985) in Bub 1985:50. The changed structures in the stripe are easily seen.

Illustr. 3. The wing feathers from a Red-billed Leiothrix (*Leiothrix lutea*) with a "fault spot" in primary 7. Photo: Wolf Dieter Busching.

Illustr. 4. Tail feathers from a Grey-headed Bullfinch (*Pyrrhula erythaca*). It is visible how the barbs break off at the places where fault bars have been, not only at the tip of the feathers but also further down the feathers. This is because the reduction in the amount of keratin renders the feather weak. It is clear that such damage must influence flight ability. Photo: Wolf Dieter Busching.

Growth bars

As fault bars are often confused with growth bars, it will be wise to start by disentangling these two terms.Growth bars were also first described by Riddle (1908) and he called them "fundamental bars". Unlike fault bars growth bars are not translucent and therefore much more difficult to recognise. Their visibility varies from family to family, e.g. in the crow family they are very easy to see (own obs.). Even within a species there can be great differences, for example in the common House Sparrow (*Passer domesticus*) (own obs.). For all, however, it is a rule that a growth bar is only visible in certain light angles and therefore it gives it some similarity with a watermark in a paper (Illustr. 5).

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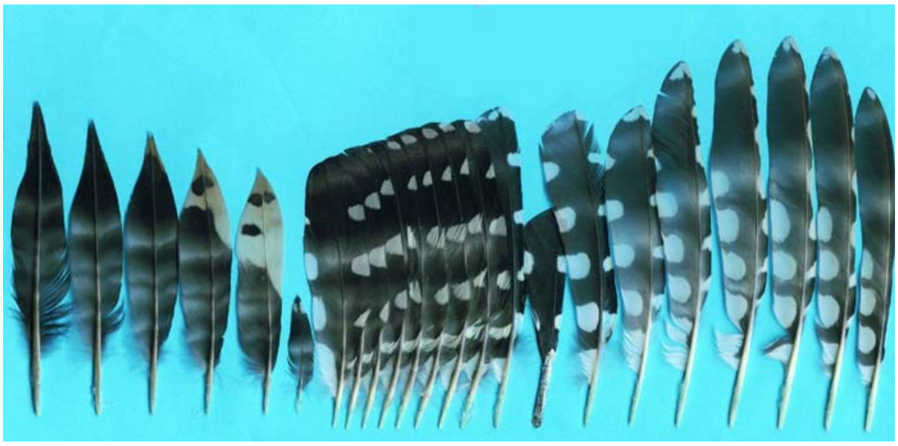
llustr. 5. Tail feathers with clearly seen growth bars. Left Olive-Backed Pipit (*Anthus hodgsoni*), right Northern House Martin (*Delichon urbica*). Photos Wolf Dieter Busching.

On colourful and marbled feathers growth bars are not easy to find and unlike fault bars they are not often visible from both sides of the feather. They are seen as alternately dark and pale cross bands running over both inner- and outer web of wing- and tail feathers, more rarely visible on other contour feathers. The dark bands are built during day the pale bands during night. Together they represent 24 hours' growth. In diurnal birds the dark band is due to a higher metabolism in the daytime when more melanin is produced (Michener & Michener 1938, Wood 1950). The difference in the width of the bands is probably due to variation in the food intake during the period of feather growth (Grubb 1989, 1991, Møller 1996). Unlike fault bars it seems that growth bars do not harm the stability of the feathers.

Terminology for growth bars and fault bars

In German growth bars are termed Wachstumstreifen and fault bars Hungerstreifen. Sadly, it isn't so simple in English: Growth bars are here also called ribbings, subordinate bars, watered barring and feather bars, and formerly they were called fundamental bars, which term, however, has also wrongly been used for fault bars. Still worse to fault bars: they are also termed hunger streaks, hunger faults, hunger traces, feather marks, starvation marks or subordinate bars and veterinary surgeons call them stress bars. It is understandable that with so many different terms much confusion has prevailed (Wood 1950, Erritzoe et al. in press).

Now not a word more about growth bars. A possible variant of fault bars is pale bands which are sometimes seen on wing- and tail feathers and which are probably due to reduced metabolism with less melanin deposition during the growth of feathers. In 99 plucks from the Great Spotted Woodpecker (*Dendrocopus major*) Bushing (2000) found no less than nine with a whitish band on both wing- and tail feathers. All nine woodpeckers were young birds in their first juvenile plumage. In my own work I have also seen this phenomenon in many different species (Illustr. 6).



Illustr. 6 Tail- and wing feathers from a young Great Spotted Woodpecker (*Dendrocopus major*) with pale cross bands. Photo: Wolf Dieter Busching.

The cause of fault bars

Fault bars are due to a developmental process that clearly has gone wrong when a fault bar is produced (Møller et al. in prep.) It is produced under stressful and adverse environment conditions. Until now the following causes have been described: hunger, bad weather, handling by man, stress in smallest nestling, human disturbance, no access to safe shelter and fragmented habitats (Erritzøe & Busching 2006).

Formerly, i.e. until a few decades ago, hunger was the generally accepted cause of fault bars, but of course hunger during the period when the new feathers are growing. This hypothesis was supported by Slagsvold (1982), Harrison (1985) and Newton (1986). In this way Newton found that the nestlings of Sparrow Hawk (*Accipiter nisus*) had more fault bars on rainy days, because they got less food, and Slagsvold saw how undernourished young of Carrion Crows (*Corvus corone cornix*) both got more fault bars and albino feathers, and Harrison in Campbell and Lacks *Dictionary* (1985) mentioned hunger as the only cause.

Unlike the Sparrowhawk young Ospreys (*Pandion haliaetus*) were not so sensitive, because even in bad weather they didn't produce any fault bars (Machmer et al. 1992).

A study by Murphy et al. (1989) seems to show that lack of food cannot be the sole cause of fault bars. For he and his team discovered among 44 White-crowned Sparrows (*Zonotrichia leucophrys*) from America, which all didn't get any food for 36 hours during which they lost 19% of their weight. In spite of this only 19 produced fault bars, and all 19 had - unlike the rest - been caught and examined in the hand! But all birds had built structurally defective feather edges which looked as if they had been shaved along the sides.

Machmer et al. (1992) recognised that young Ospreys, which were often handled and examined, produced much more fault bars than a control group which either had few visits or none at all. They also saw that the smallest nestling, which as is well known has the lowest status, also had most fault bars. The same result was reached by Negro and his team (1994), who in the American Kestrel studied the connection between food and stress from handling. Fröhlich (2005) researched 2004/05 how the feathers grew in 17 Brown Skua (*Stercorarius antarctica*) chicks from hatching until fledging, and also their food was checked. She too came to the same conclusion.

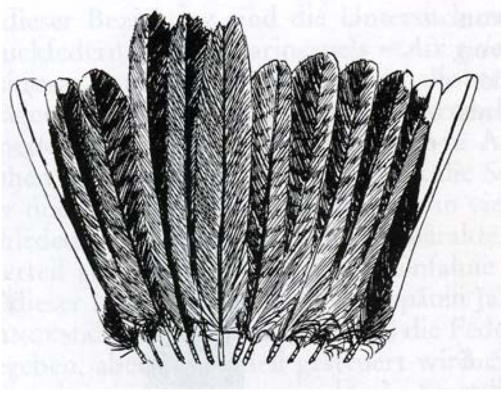
All the cases mentioned here produce stress in an individual, of course also hunger, and as is well known, stress releases a cascade of psychological spontaneous reactions which can all be tracked in the metabolic process (Buchanan 2000). Moreover, an organism under stress uses more energy than one without stress ((Møller & Swadde 1997). Increased energy spent on metabolism causes changes of the said psychological reaction, which disrupts the formation of feathers. A consequence of this could for example be feather asymmetry. The following is an example of this: A group of Starlings (*Sturnus vulgaris*) was kept in a sterile aviary without any possibility of cover. These birds grew more asymmetric feathers and fault bars than a control group which had dense vegetation in their aviary with many hiding places (Witter & Lee 1995, Sommer 1996, in: Leung et al. 2000). Birds in fragmented forests also produce more asymmetric feathers (Lens et al. 2002) and fault bars (Sodhi 2002).

As moulting is a very energy demanding process it normally occurs in a period when there are no other demanding tasks like breeding or migration for adult birds, but when there is still plenty of food; or in sedentary birds the moult is often spread over many months or even the entire year (Cramp & Simmons 1977-1994). In nestlings, however, the period when the feathers are growing out is a very sensitive time of their life, because at the same time they have to grow, and therefore the chicks react strongly by producing fault bars even under weak forms of stress. In young White Storks (*Ciconia ciconia*) Jovani & Blas (2004) found three times as many fault bars as in adult birds. Also young Barn Swallows (*Hirundo rustica*) have more fault bars than the adults (Serrano & Jovani 2005), and common House Sparrow (*Passer domesticus*) fledglings may have more than one hundred fault bars only in their wing- and tail feathers when breeding close to humans with much disturbance (unpublished own obs.).Other authors have also described more fault bars in young birds (Slagsvold 1982, Hawfield 1986, Jovani & Blas 2004).

Another interesting case is the different amount of fault bars in the two sexes. In the American Kestrel Dawson et al. (2001) found that the female had more fault bars than the male. He explained this with the greater stress the female is exposed to during the breeding season.

It is supposed that fault bars in adults can sometimes reflect conditions of the previous summer. For example Barn Swallows, which one summer had got their tail feathers manipulated longer, showed more fault bars following moult the next year (Møller 1989). As is well known, female Barn Swallows prefer partners with long tail streamers because these signals good genes (Møller 1994). Therefore it is easy to imagine the stress such a male with fake sex characters may experience when continually courted by the other sex and flying with exaggerated tail feathers.

An interesting theory has been published by King and Murphy (1984), who propose that there is a connection between fault bars and fright moult. According to their assertion a shock or a fright should provoke a spontaneous convulsive contraction of the ring muscle which surrounds a growing feather, which still has a soft substance, and this should cause a stunting of the barbules in the actual growing place. Not so as to fright moult. Here we have to do with a finished, hard and dead feather. In such cases the contraction of the ring muscle resulting from a shock did not lead to stunting of the feather, but to a spontaneous shedding. The new feather growing out on the place of the one shed is always shorter, and because it is growing slower, the growth bars are also narrower (Larianow 1935 and Illustr 7).



llust. 7. Drawing of tail feathers of a Great Tit (*Parus major*) with nine regrown feathers due to fright moulting. Not till the next moulting will the feathers grow out to their normal length. (Busching 2005: 34)

Fault bars as an indication of the bird's health and as a sign of success by partner choice and breeding.

Fault bars are visible at a short distance and probably serve as a sign for the female of the health and fitness of the male. It is documented that American Kestrels with many fault bars have poor body condition, are less likely to breed and have shorter lives. However, surprisingly there are no negative consequences regarding clutch size or egg size (Bortolotti et al. 2002). Common Magpies (*Pica pica*) with perfect tail feathers have larger gonads and produce more fledglings than a pair with damaged tails. Besides a one-year-old Common Magpie with long tail feathers had a better immune system than others with shorter tails (Fitzpatrick & Price 1997, Blanco & de la Puente 2002.

However, it is important to note that two individuals of the same species which both experience the same stress factors may have different resistance and therefore show different reactions (Buchanan 2000). Research in the American Kestrel has thus shown that from year to year the same individual produce the same number of fault bars. This could be a hint that maybe birds have a stress tolerance, high or low (Bortolotti et al. 2002).

Barn Swallow males with normal long tail feathers have fewer fault bars than males with shorter tails. By contrast in females there was no difference in the number of fault bars between those with long and short tails (Møller 1994). These few examples support the hypothesis that missing fault bars are a sign of good genes, and that the female uses it when she chooses a partner.

Natural selection and its influence on the fault bar phenomenon

The feather structure becomes weaker with many fault bars. The feather often breaks in the place where the fault bar is located and the feather will not be renewed before next moult (Dawson et al. 2001) (see Illustr. 4). Therefore it is a great handicap for a bird because an individual with many fault bars is less manoeuvrable and becomes an easier target for a predator (Murphy et al. 1989). For example the frequency of fault bars in prey of the Northern Goshawk was almost three times higher than in the population, demonstrating that predation selects strongly against fault bars (Møller et al. in prep.).

A new hypothesis, "the fault bar allocation hypothesis" predicts, that a bird can develop adjustment mechanisms that reduce fault bars on feathers that are important for flying (Jovani & Blas 2004). And see if that does not turn out to be the case, indeed! A study of White Storks has shown that the distribution of fault bars was arranged with most of them on the inner wing feathers that have less importance for flight ability (JOVANI & BLAS 2004), whereas in the flightless Ostrich (*Strutio camelus*) fault bars were evenly distributed on all contour feathers (Duerdan 1909, in: Jovani & Blas 2004). As a rule fault bars are found more often in tail- than in wing feathers and in the wings particularly in the inner secondaries and tertials. These feather types are, as already mentioned, of less importance for manoeuvring because they have to handle a smaller mechanical load than primaries (Slagsvold 1982, King & Murphy 1984, Machmer et al. 1992, Bortolotti et al. 2002, Serrano & Jovani 2005, Sarasola & Jovani 2006 and own obs.).

Illustr. 8. Tail feathers from a Saker Falcon (*Falco cherrug*). The two feathers to the right have some fault bars at the tip and the outermost tip is abnormal. The left feather is from the same individual but from the next year when the feather does not show any deformity. Photo: Wolf Dieter Busching.

But natural selection does not end here. In a Danish study of prey taken by the Sparrowhawk nearly 32000 prey of 66 passerine species were determined (Nielsen 2004), and the result was compared with about 3,200 Danish passerine skins. The result demonstrated quite surprisingly that species most often taken as prey by the Sparrowhawk were those with fewer fault bars. This result suggest that natural selection due to predation has modifies the mechanisms that control the development of fault bars, thereby reducing the frequency of fault bars in species that are disproportionately often caught by agile avian predators (Møller et al. in press.)

For a bird that spends most of its time in the air like a Common Swift (*Apus apus*), fault bars would be a disaster. Two Swift nestlings were kept in captivity in darkness and without any food for respectively 13 and 21 days. Quite surprisingly this had no influence on the growing feathers, which didn't have any fault bars at all (Mitchell 1959). In adult Common Swift, however, fault bars are found although very rarely (Møller et al. in prep.).

Most lay people believe that "the hand of evolution", also called natural selection works perfectly by selecting the ideal solution through many thousands years and that all organisms and their characters are therefore perfect. This is not so. Becacuse I suppose that fault bars can occur in most bird families I suppose that the damage happened in an early period of the development of birds, when the very first feather structures were produced, and the "error" was afterwards transferred to all other feathered creatures. Later in the development when the stress became too great, e.g. due to intense predation, natural selection worked may have adjusted moult, for example by increasing the duration of the moulting period, in such a way that the "error" became less frequent.

As we humans fragment more and more landscapes, these fragmented areas become more and more like small islands surrounded by oceans of crops. It is a long known fact that bird species on small islands, much more than on larger islands, have a high risk of extinction. It is therefore important to follow populations in fragmented landscapes. Therefore for conservation research fault bars can maybe be an "early warning" signal of adverse conditions as experienced by free-living birds (Lens et al. 2002).

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