

Stress during feather development predicts fitness potential

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Summary

1. Measures of the quality of an individual are important in the study of proximate and ultimate factors in biology. Records of developmental history are particularly desirable, as many phenotypical traits are influenced by conditions during growth. Conspicuous irregularities in feathers, known as fault bars, result from a variety of stresses that occur during feather growth. The frequency of fault bars was evaluated on primary and tail feathers (grown 1 year previously) of 1919 adult American kestrels from a breeding population in Canada (1990–97).

2. Most (91.5%) birds exhibited some fault-barring, although females had significantly more feathers with fault bars than males (17% vs. 14%, respectively). Body size, intensity of haematozoan infections and leucocyte differentials were all unrelated to fault bars; however, birds with many fault bars were in poor body condition during prelaying (males) and incubation (males and females).

3. Individual kestrels tended to be consistent in the number of feathers with fault bars from year to year.

4. The percentage of feathers with fault bars was not associated with the timing of arrival in spring or prey abundance per territory; however, birds of both sexes with many bars were less likely to breed. Birds paired non-randomly, as mates tended to have a similar frequency of fault bars. Males and females with many bars had significantly later clutch initiation dates, but there were no negative consequences regarding clutch size or egg size.

5. Female kestrels with many fault bars had lower survival probabilities. Both sexes were also less likely to be recaptured in years following initial banding if they had many bars, suggesting that they were more likely to emigrate from the study area temporarily.

6. Fault bars on feathers appear to be indicative of an individual's susceptibility to stress, and are useful in predicting components of fitness. The use of fault bars is a promising tool as they are easy to evaluate and can be assessed on live or dead birds, on moulted feathers and on individuals repeatedly over time.

Key-words: American kestrels, condition, fault bars, reproduction

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Introduction

Biologists have given considerable attention to attributes of individuals that could be used as predictors of fitness. In particular, reliable measures of individual quality as manifested by physical condition, reproductive performance and attractiveness to mates have been sought (e.g. Brown 1996; Fitzpatrick & Price

1997; Catry *et al.* 1999; Buchanan 2000). While physiological measures, including popular haematological and immunological variables (e.g. Dawson & Bortolotti 1997; Tella *et al.* 2000a), are useful for evaluating current or recent states, their reliability in evaluating an individual's potential is more limited. Some morphological characters, such as body size and colour, have shown merit as predictors of some components of fitness (e.g. Hill 1991; Nolan, Hill & Stoehr 1998; Barbosa & Møller 1999).

Many phenotypical traits of adults are strongly influenced by conditions experienced during development, and so attention is being given increasingly to

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how such conditions may have long-term fitness consequences (Lindström 1999). Considerable success in evaluating the quality of individuals has been achieved by using variables that act as records of past developmental events. Currently, a popular evaluator is fluctuating asymmetry – a measure of developmental stability (Møller 1993); however, the deviations from symmetry are typically small, inconsistent among characters, and there are concerns over how results are interpreted (Bjorksten, Fowler & Pomiankowski 2000; Leung, Forbes & Houle 2000). There are alternative methods for evaluating developmental history, using feathers, that show great promise.

Feathers offer some unique opportunities for evaluating an individual bird's quality. They have the distinct advantage of being replaced in a predictable fashion and on a time scale, typically annually, that allows for assessment of developmental history of mature birds as well as nestlings, and of individuals repeatedly over time. Because materials are not deposited in a growing feather in a uniform or invariable fashion, there are conspicuous qualitative differences within and among individual feathers and individual birds (Murphy, Miller & King 1989). In recent years, ptilochronology – the measurement of growth bars, has emerged as a technique whereby the rate of elongation of feathers can be quantified (Grubb 1995). These bars are faint bands that correspond to diurnal and nocturnal growth, and so allow the nutritional state of a bird to be assessed. Feathers are also known to vary qualitatively in another fashion useful in the assessment of developmental history, i.e. fault bars.

Unlike growth bars, which are not obvious on all feathers or all species (Grubb 1995), fault bars are much more conspicuous. They are seen as streaks of frayed or missing vane running approximately perpendicular to the rachis. Fault bars form on growing feathers and are the result of abnormally formed or missing barbules and vary in severity, such that some vanes show light lines while others have conspicuous holes (Murphy *et al.* 1989). Breakage of the feather is more likely to occur at such points (Newton 1986; personal observation). Many feathers have multiple fault bars, and generally they are more common on rectrices than remiges (Slagsvold 1982; Hawfield 1986; but see Negro, Bildstein & Bird 1994). For many populations, such marks are present on the majority of individuals (e.g. Slagsvold 1982; Newton 1986; this study). Fault bars have been particularly well documented in the scientific study and falconry lore of raptors (Negro *et al.* 1994), but are viewed broadly for all bird species as an indicator of stress. In fact, alternative common names for this phenomenon are stress marks, fret marks and hunger traces (Doolen 1999). Despite a long folklore surrounding fault bars and their recent acknowledgement in avian clinical practice (Ritchie, Harrison & Harrison 1994; Doolen 1999), our understanding of their causes and consequences is rudimentary. Fault bars have been associated with low endogenous (Slagsvold 1982) or

exogenous (Waite 1990) energy reserves. While the incidence of fault-barring has also been used to reveal the physiological cost of ornamental feather growth (Andersson 1994), future fitness correlates of feather quality remain untested. We use the American kestrel (*Falco sparverius*, Linnaeus), a small monogamous falcon, as our model and present evidence for fault bars being indicative of the quality of individuals and predictors of various components of fitness.

FORMATION OF FAULT BARS

Food-related stress has been evoked commonly as the probable cause of fault-barring (Slagsvold 1982; Newton 1986; Machmer *et al.* 1992). However, Negro *et al.* (1994) concluded that handling stress had a greater effect on fault-bar formation in captive, nestling American kestrels than did periodic food deprivation (see also King & Murphy 1984; Murphy *et al.* 1989). Negro *et al.* (1994) suggested that in free-ranging birds nutritional stress typically co-occurs with other forms of stress such as periods of cold and rain (see also Newton 1986; Machmer *et al.* 1992). Apparently (i.e. no data presented) fault bars can be induced by the administration of glucocorticoids, further suggesting a role for 'stress' (Doolen 1999). Clinicians propose that any stress – starvation, poor nutrition, environmental changes, dehydration, infection, chilling, overheating, restraint and even emotional turmoil in the home of a pet bird – can induce fault bars in growing feathers (Ritchie *et al.* 1994; Doolen 1999). Clearly, these feather aberrations provide a record of challenges to a bird's homeostatic state. Just as the adrenocortical response is generalized to an array of stressors (Buchanan 2000), so are fault bars, and perhaps the two are related mechanistically.

In this study, feathers were months old upon examination. Specifically in our area (see Methods), remiges and rectrices of kestrels examined by us at the onset of one breeding season in April were grown from May to September or later of the previous year. Fault bars are thus a lasting record of multiple stress events over a long period of time. As such they may be a good overall measure of how birds cope with the many challenges of life, and hence an indicator of fitness potential.

Methods

CAPTURE AND FEATHER EVALUATION

A population of 150–200 pairs of American kestrels breeding in nestboxes near Besnard Lake, Saskatchewan (55°N, 106°W) was studied from 1990 to 1997. Kestrels arrived from migration in mid- to late April, and breeding commenced in mid-May. Prior to egg laying bal-chatri traps were used to capture kestrels (Murza, Bortolotti & Dawson 2000), while during incubation birds were captured by hand in nestboxes. It is unlikely that a condition bias existed for the use of a

baited trap, as there was little evidence for such even for kestrels with substantial physical handicaps (Murza *et al.* 2000). Each bird was given a unique combination of three coloured plastic leg bands and a numbered aluminium leg band. Primary remiges and rectrices of each bird were inspected for the presence of fault bars and all bars were drawn on a diagram so that number and position were recorded. Also recorded was whether any feathers were missing or broken. Because birds with missing or broken feathers had fewer feathers inspected, the percentage of feathers that had fault bars was used for analyses. It is important to note that the feathers inspected were grown 8–12 months earlier. Moulting of primaries begins shortly after incubation has commenced, with females starting somewhat before males (Bird 1988; G. R. Bortolotti & R. D. Dawson, unpublished data). However, the rectrices (where most fault bars were observed) were grown primarily in August when offspring were still dependent on their parents, and during migration in August and September and perhaps later, based on our observations of breeding birds and captures of migrants.

To determine if birds with more fault bars arrived on the study area later in the season than those with few fault bars, prelaying capture date was used as a surrogate for arrival date. During the prelaying period of each year, we monitored the entire study intensively for the appearance of kestrels on territories (Bortolotti & Iko 1992). Upon occupying a territory, both sexes perch conspicuously near a box and we believe that most birds were captured soon after their arrival.

From 1993 to 1997, each bird was weighed (nearest g) and six measures of size were recorded: lengths of the unflattened wing chord, central rectrix, outer rectrix, and tenth primary (nearest mm), length of the exposed culmen, and width of the tarsus (nearest 0.1 mm). Body size was estimated for each sex separately (males, $n = 406$; females, $n = 596$) using a principal components analysis; linear size measurements were input variables, and the first component (PC1) was the estimate of size (see Bortolotti & Iko 1992). Body size was evaluated as it is a potential correlate of both condition and of fault barring (Slagsvold 1982). To obtain an index of body condition we first removed the confounding effect of body size by using the residuals from a regression between mass and PC1 (males: $r = 0.29$, $F_{1,404} = 36.52$, $P < 0.0001$; females: $r = 0.17$, $F_{1,594} = 17.00$, $P < 0.0001$). This measure of condition has been shown repeatedly to correlate positively with a number of components of reproductive performance and the well-being of individuals in this population (e.g. Bortolotti & Iko 1992; Wiebe & Bortolotti 1995; Dawson & Bortolotti 2000; Tella *et al.* 2000a).

BLOOD SAMPLING

In 1994 and 1995, blood collected from either the brachial or jugular vein was used to make blood smears (see Dawson & Bortolotti 1999, 2000). Smears were air-

dried and fixed immediately in 100% ethanol. Intensity of haematozoan infections was determined at the International Reference Centre for Avian Haematozoa at Memorial University, St John's, Newfoundland, Canada by counting the number of parasites in 100 microscope fields under oil, using a 100× objective lens for *Haemoproteus* and *Plasmodium*, and 40× objective for *Leucocytozoon* and *Hepatozoon*. For the determination of leucocyte differentials, blood smears collected in 1997 were stained with Wright–Giemsa stain and the total white blood cell count (WBC, cells $\times 10^9$ per litre) was estimated by taking the average number of leucocytes in five fields observed under 40× lens. WBC was standardized to the number of red blood cells, and to control for variability in smear preparation the fields selected were in an evenly distributed monolayer. The proportions of heterophils, lymphocytes and the heterophil/lymphocyte ratio (H/L) were determined by identifying 100 cells under 40× power.

REPRODUCTIVE PERFORMANCE

From 1993 to 1997, nestboxes were visited every 3–5 days from mid-May to mid-June. Once the first egg was laid, we waited until the clutch was complete and then revisited the nest to record clutch size. Kestrels lay eggs every 2 days (Bortolotti & Wiebe 1993) so it was possible to determine clutch initiation date ± 1 day. From 1994 to 1996, the length and width of each egg was measured with dial callipers (nearest 0.1 mm) and egg volume was calculated (volume = length \times width² \times 0.51) (see Wiebe & Bortolotti 1995). For analysis, we used mean volume of all eggs in individual completed clutches. The number of fledged offspring was not analysed here as broods were subjected frequently to experimental manipulation (e.g. Tella *et al.* 2000a).

ABUNDANCE OF SMALL MAMMALS

The abundance of food on each kestrel territory was assessed between 1993 and 1997 by censusing the main prey of kestrels, small mammals (Bortolotti *et al.* 2000). During the prelaying (early May) and brood rearing (early July) periods, trap lines consisting of 10 stations spaced 30 m apart and situated parallel to, and 10 m from a road, were set on kestrel territories. At each station two snap traps were baited with peanut butter. Each line operated for 3 days, and traps were reset each morning. Data were standardized to mean number of animals per 100 trap-nights. Mammalian prey of kestrels during brood rearing consisted primarily of red-backed voles (*Clethrionomys gapperi*); however, results were identical whether all small mammal numbers or only numbers of voles were used as the index of prey abundance. Only results using all small mammals are presented here. This index might seem to be a coarse measure of food abundance, but it correlates well with variation in many aspects of reproductive performance (Bortolotti, Wiebe & Iko 1991; Wiebe & Bortolotti 1994, 1995).

STATISTICAL ANALYSIS

For most analyses, birds were categorized as having either 'many' or 'few' fault bars, according to whether their percentage was above or below 20%; i.e. above or below the mean. The difference between these two categories may be larger than it appears using our classification, as generally we found that birds with many feathers with bars tended to have many fault bars per feather (see also Slagsvold 1982). With the exception of analyses concerning change in fault bars between years within individuals, all analyses use only the first captures of individual birds to ensure independence of data points.

Annual variation and differences between the sexes with regard to percentage of feathers with fault bars was tested with ANOVA, while the numbers of males vs. females classified as having few or many fault bars was tested with a *G*-test. For birds captured in multiple years, the percentage of feathers with fault bars at the first capture was compared to the percentage at the second capture using correlation analysis. The consistency of fault bars within individuals was examined further by comparing barring at the time of the first and second captures, as well as the second and third captures, using paired *t*-tests.

Whether body size (PC1, see above) affected the probability of a bird being classified as having many or few fault bars was determined using a logistic regression; fault bar category was the binary dependent variable, with PC1 and year as independent variables. To analyse whether fault bars were related to body condition, spring arrival date, food abundance on territories in May or July, clutch initiation date, clutch and egg size, intensity of blood parasite infection and leucocyte differentials, we used a series of ANOVAs with fault bars (few vs. many) and year as independent variables (some specific details below). For these analyses, non-significant interactions and terms in models were removed iteratively and analyses repeated to obtain the most parsimonious models that explained variation in dependent variables; however, the independent variable of interest, fault-bar category, was always retained in final models.

For analysis of body condition of males, capture date was included as a covariate in the model because condition increases seasonally (Dawson & Bortolotti 1997). Body condition of females increased rapidly with the onset of clutch initiation (Dawson & Bortolotti 1997), so body condition of females was evaluated separately for prelaying and incubation periods. Statistical analysis of incubating females was similar to that of males, whereas for prelaying females, a cubic regression was performed between body condition and the number of days before egg laying that females were captured ($R^2 = 0.45$, $F_{3,150} = 40.75$, $P < 0.0001$) (see also Dawson & Bortolotti 1997). The residuals from the cubic regression were then used as a corrected measure of condition (see also Dawson & Bortolotti 2000).

Whether or not the degree of fault-barring influenced the likelihood of a bird breeding was tested for kestrels captured between 1993 and 1997. Each bird was classified according to whether or not it was associated with a nest that contained at least one egg, and these groups were compared according to fault-bar category with a *G*-test. For mated pairs, whether birds with few fault bars were more likely to obtain mates with few as opposed to many fault bars was tested with a *G*-test. Analyses were performed using SPSS (Norusis 1993) and SAS (SAS Institute Inc. 1988). We present means ± 1 SE, and all tests are two-tailed unless otherwise noted.

We estimated local adult survival (ϕ) and recapture rates (p) for each sex separately using a modified Cormack–Jolly Seber procedure for open populations (Lebreton *et al.* 1992; Burnham & Anderson 1998). Models were developed and evaluated using program MARK (White & Burnham 1999), and model notation follows Lebreton *et al.* (1992). We first developed a fully parameterized global model for each sex that allowed both survival and recapture probability to vary with fault bar category (i.e. a group effect: few vs. many fault bars), year (i.e. time dependency), and the interaction between fault bars and year ($\phi_g \times t p_g \times t$). Goodness-of-fit (GOF) of the global model to the data was evaluated using the parametric bootstrapping approach available in program MARK. The global model and all possible reduced parameter models were included in the set of candidate models; overall, we evaluated 25 models for each sex. Model selection was based on the comparison of Akaike information criterion (AIC) adjusted for overdispersion and sample size (QAIC_c; Lebreton *et al.* 1992; Burnham & Anderson 1998):

$$\text{QAIC}_c = \frac{-2 \ln(L)}{\hat{c}} + 2np + \frac{2np(np+1)}{n_{\text{ess}} - np - 1}$$

where L is the model likelihood, np is the number of estimable parameters, n_{ess} is the effective sample size, and \hat{c} is the variance inflation factor that adjusts for overdispersion in data. The value for \hat{c} was estimated as the quotient of the observed model deviance and the mean deviance computed from 1000 bootstrapped simulations during GOF testing (above). When the model fits the data perfectly, $\hat{c} = 1$.

The model with the lowest QAIC_c was taken to be the most parsimonious for the data; however, models with QAIC_c values that differed from the model with the lowest QAIC_c by less than 2 were also considered to fit the data equally as well (Burnham & Anderson 1998). Model comparisons were also accomplished by calculating relative plausibility using normalized Akaike weights. Weights for each model were calculated as $w_i = \{\exp(-\Delta\text{QAIC}_c/2)\} / \{\sum \exp(-\Delta\text{QAIC}_c/2)\}$, where ΔQAIC_c is the numerical difference between the QAIC_c weight of a particular model and that of the model with the lowest QAIC_c. The ratio of w_i between two models provides an estimate of the relative degree that one model is better supported by the data than the other

model. To take uncertainty in model selection into account, we used model averaging to derive estimates of survival and recapture probability. This procedure involves estimating survival and recapture parameters (θ) by taking an average of parameters (θ_i) from all models in the candidate set, weighted by their relative plausibility (normalized Akaike weights, w_i): $\text{avg}(\theta) = \sum w_i(\theta_i)$.

Results

FAULT BAR ABUNDANCE AND ATTRIBUTES OF BIRDS

Between 1990 and 1997, fault bars were quantified on 1919 individual kestrels. Some degree of barring was evident on the flight feathers of most (91.5%) birds. On average, 16.8% (± 0.40 , range 0–100%, $n = 1157$) of the primary rectrices and remiges of females, and 13.6% ± 0.42 of the feathers of males (range 0–75%, $n = 762$) had fault bars. ANOVA revealed highly significant effects attributable to sex ($F_{1,1903} = 35.92$, $P < 0.001$) and year ($F_{7,1903} = 33.25$, $P < 0.001$). There was also a significant sex \times year interaction ($F_{7,1903} = 2.68$, $P = 0.009$). This latter result appears to be largely a product of near equal fault-barring between the sexes in 1990. When that year was removed and the ANOVA repeated there was no significant interaction effect, but sex and year retained their significance ($P < 0.001$). Highly significant sex differences were also apparent when we classified birds into categories of few and many bars ($G = 27.0$, d.f. = 1, $P < 0.001$).

Using PC1 as a measure of size, we found no effect of body size from 1993 to 1997 on the probability of a bird being classified with few and many fault bars for either sex (logistic regressions, males: $\chi^2 = 1.75$, d.f. = 1, $P = 0.19$; females: $\chi^2 = 2.33$, d.f. = 1, $P = 0.13$). Body condition of male kestrels showed significant annual variation ($F_{4,390} = 3.24$, $P = 0.01$), and increased seasonally, as indicated by the positive relationship with date of capture ($F_{1,390} = 17.98$, $P < 0.001$). In addition, condition of males was significantly lower for males with many fault bars compared to those with few fault bars ($F_{1,390} = 6.62$, $P = 0.01$; Fig. 1). After controlling for breeding chronology, we could detect no differences in condition during prelaying between females with few or many fault bars ($F_{1,150} = 0.21$, $P = 0.64$). Condition of incubating females declined with capture date ($F_{1,275} = 22.90$, $P < 0.001$) and tended to be lower among females with many fault bars compared to those with few fault bars ($F_{1,275} = 3.63$, $P = 0.058$; Fig. 1).

Of birds that returned in years following initial capture, there was a significant positive relationship between the percentage of feathers with fault bars at first capture and the percentage with fault bars at second capture (males: $r = 0.26$, $n = 88$, $P = 0.02$; females: $r = 0.27$, $n = 116$, $P = 0.003$), suggesting that fault barring was consistent within individuals among years. This was confirmed when fault bars between capture

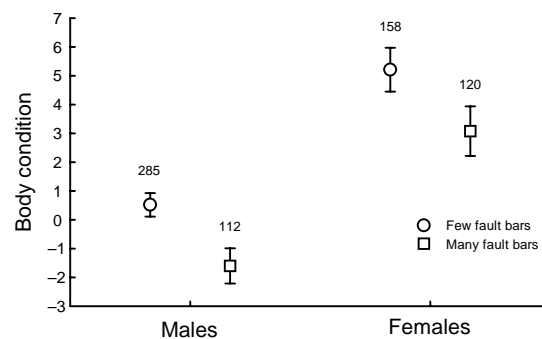


Fig. 1. Mean body condition \pm SE of male and incubating female American kestrels according to whether their remiges and rectrices had few or many fault bars. Body condition is the residual from a regression between body mass and body size. See Methods for further details. Sample sizes are indicated above error bars.

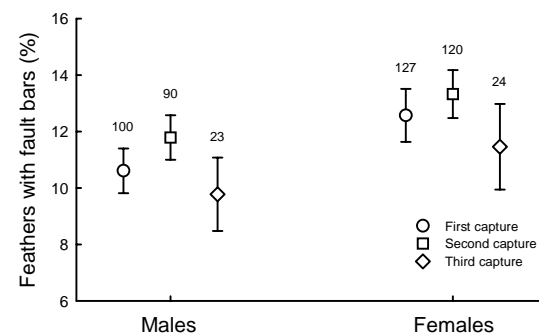


Fig. 2. Mean percentage of remiges and rectrices \pm SE that had fault bars among birds that were captured two and three times over the course of the study. Sample sizes are indicated above error bars.

years were compared within individuals. The percentage of feathers with fault bars did not change either between the first and second capture (paired t -tests, males: $t = -0.46$, d.f. = 87, $P = 0.65$; females: $t = -0.94$, d.f. = 115, $P = 0.39$), or between the second and third captures (paired t -tests, males: $t = 0.75$, d.f. = 20, $P = 0.46$; females: $t = 0.56$, d.f. = 20, $P = 0.58$) (Fig. 2).

PARASITES AND LEUCOCYTE DIFFERENTIALS

The differences in condition according to fault-bar classification for males and incubating females was not the result of differential blood parasitism. Intensity of infection by *Haemoproteus*, detected in 85% of birds (Dawson & Bortolotti 1999), was not different between birds with many or few fault bars before egg laying (males: $F_{1,52} = 0.78$, $P = 0.38$; females: $F_{1,95} = 0.15$, $P = 0.70$), during incubation (males: $F_{1,65} = 0.01$, $P = 0.97$; females: $F_{1,66} = 1.82$, $P = 0.18$), or when parasite data for both periods were pooled (males: $F_{1,119} = 0.47$, $P = 0.49$; females: $F_{1,164} = 0.01$, $P = 0.93$). The difference in condition associated with fault bars could also not be attributed to exposure to pathogens according to the analysis of leucocyte differentials. For the birds captured in 1997 when leucocytes were quantified,

ANOVA or ANCOVA (with date as a covariate when it was significant) was used to test for effects of fault bar category. We could not detect any difference between fault-bar categories with respect to H/L ratio, the counts and percentages of heterophils or lymphocytes, or total WBC (all P s > 0.1).

ARRIVAL DATE AND TERRITORY QUALITY

There was significant annual variation in spring arrival dates of males on the study area between 1993 and 1997 ($F_{4,185} = 7.16$, $P < 0.001$), but the abundance of fault bars was not related significantly to arrival date ($F_{1,185} = 1.38$, $P = 0.24$). Similarly, arrival dates of females varied annually ($F_{4,284} = 5.01$, $P = 0.001$) but were unrelated to whether females had few or many fault bars ($F_{1,284} = 0.01$, $P = 0.97$).

Food abundance on territories of kestrels can be an important determinant of reproductive success. Therefore, prior to testing for relationships between fault bars and reproductive performance, it was determined, first, whether territory quality differed according to fault-bar category. Perhaps because of their simultaneous arrival in spring, we could not detect any relationship between fault-bar category and the quality of territory measured as number of small mammals in May (males: $F_{1,40} = 0.01$, $P = 0.92$; females: $F_{1,66} = 1.91$, $P = 0.17$). Similarly, there was no difference in prey abundance between birds with few or many fault bars during July when young were in the nest, although significant annual variation existed for both males (year: $F_{4,112} = 4.14$, $P < 0.01$; fault bar category, $F_{1,112} = 1.18$, $P = 0.28$) and females (year: $F_{4,179} = 5.11$, $P < 0.001$; fault-bar category: $F_{1,179} = 0.07$, $P = 0.80$).

MATED PAIRS

Only 16% (32 of 195) of females with few fault bars had mates with many fault bars. In contrast, 69% (77 of 111) of females with many fault bars also had mates with many fault bars, suggesting that kestrels were pairing assortatively ($G = 8.22$, d.f. = 1, $P < 0.01$). Similarly, the percentage of feathers with fault bars were significantly correlated within mated pairs ($r_s = 0.15$, $n = 306$, $P = 0.009$).

If poor-quality kestrels obtain poor-quality mates as suggested by Bortolotti & Iko (1992), then some individuals may not find mates at all, or may be unable to acquire sufficient resources to lay. Therefore, it was predicted that birds that had a record of stress would be less likely to be identified as breeders than those that did not, and so a one-tailed statistical test was used. There was weak support for this prediction as 70% ($n = 297$) of males with few fault bars bred on the study area compared with 63% ($n = 116$) of males with many fault bars ($G = 1.72$, d.f. = 1, $P = 0.09$). Similarly, 80% ($n = 336$) of females with few fault bars bred, whereas 75% ($n = 291$) of those with many fault bars bred ($G = 2.37$, d.f. = 1, $P = 0.06$).

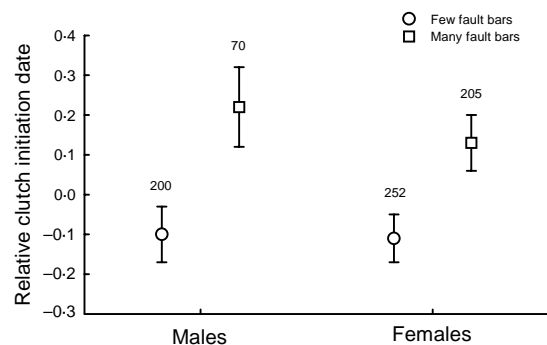


Fig. 3. Mean clutch initiation dates \pm SE of female American kestrels and mates of male kestrels according to whether their remiges and rectrices had few or many fault bars. Clutch initiation dates were standardized for each year separately by calculating Z-scores. Sample sizes are indicated above error bars.

REPRODUCTIVE PERFORMANCE

The relationship between clutch initiation date and fault bar category was investigated after initiation dates were standardized for each year separately using Z-scores. Female kestrels with many fault bars laid significantly later in the season than those with few fault bars ($F_{1,455} = 6.42$, $P = 0.01$; Fig. 3). Similarly, male kestrels with many fault bars had mates that laid significantly later in the season than those with few fault bars ($F_{1,268} = 5.35$, $P = 0.02$; Fig. 3).

For analyses of clutch and egg size, we included clutch initiation date as a covariate to control for potential seasonal variation. Clutch sizes varied significantly among years ($F_{4,436} = 5.67$, $P < 0.001$) and declined significantly with initiation date ($F_{1,436} = 32.58$, $P < 0.001$); however, there was no difference in clutch sizes between females with many and few fault bars ($F_{1,436} = 0.37$, $P = 0.55$). The relationship between clutch size and fault bars of males was similar; there was annual variation in clutch size ($F_{4,248} = 5.45$, $P < 0.001$) as well as a seasonal decline ($F_{1,248} = 16.08$, $P < 0.001$), but no difference between birds with many or few fault bars ($F_{1,248} = 1.91$, $P = 0.17$). Mean volume of eggs was not different between females with many or few fault bars ($F_{1,200} = 1.00$, $P = 0.32$). For males, there was a significant seasonal decline in the size of eggs laid by their mates ($F_{1,137} = 5.72$, $P = 0.02$), but egg size was not dependent on fault-bar status ($F_{1,137} = 0.70$, $P = 0.41$).

Because reproductive success is the result of the contributions of the male and female, and given significant assortative mating (see above), we analysed the reproduction variables again using ANOVA or ANCOVA as appropriate but using the combination of fault-bar categories for male/female of: few/few, few/many, many/few and many/many. All results were identical to the single-parent analysis, i.e. significant effects of fault bars on initiation date ($F_{3,293} = 3.38$, $P = 0.019$) but not clutch and egg sizes. Although the contribution of a poor-quality male alone or female alone were similar

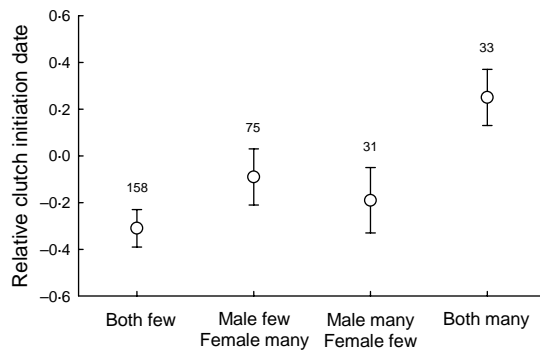


Fig. 4. Mean relative clutch initiation date \pm SE for mated pairs of American kestrels of different combinations of categories of few and many fault bars. Sample sizes are indicated above error bars.

Table 1. Summary of mark–recapture models of apparent survival and recapture probabilities of American kestrels in Saskatchewan. Models are ordered by increasing QAIC_c value. Subscript ‘g’ refers to a grouping factor in the models (few or many fault bars). *np* refers to number of parameters estimated. Of 25 possible candidate models for each sex, only those with QAIC_c weights > 0.05 are listed

Sex	Model	QAIC _c	Δ QAIC _c	QAIC _c weight	<i>np</i>	Deviance
Females	{ ϕp_g }	838.33	0.00	0.41	3	77.20
	{ $\phi_g p$ }	838.62	0.29	0.36	3	77.49
	{ $\phi_g p_g$ }	839.76	1.43	0.21	4	76.62
Males	{ $\phi_g p_g$ }	668.52	0.00	0.47	4	84.31
	{ ϕp_g }	669.62	1.10	0.27	3	87.42
	{ ϕp }	671.54	3.02	0.10	2	91.36

and intermediate between the few/few and many/many categories (Fig. 4), a posteriori tests (Scheffé’s) could only detect significant differences between pairs with few/few and many/many fault bars ($P < 0.05$).

SURVIVAL AND RECAPTURE PROBABILITIES

From 1990 to 1996, 1047 female and 696 male kestrels were marked and released. Of these, 104 males and 127 females were resighted or recaptured at least once between 1991 and 1997. Goodness-of-fit tests suggested that our global model fit the data adequately for both sexes ($P > 0.05$) and that there was relatively little evidence for overdispersion in our data sets (males: $\hat{c} = 1.02$; females: $\hat{c} = 1.07$). For females, the most parsimonious model included an effect of fault bars on recapture but not survival probability (ϕp_g); however, a

model including an effect of fault bars on survival but not recapture ($\phi_g p$) was also well supported by the data (Table 1). A third model that included a fault-bar effect on both survival and recapture probabilities ($\phi_g p_g$) also received some support (Table 1). Together, these three models had 97% of the support (i.e. sum of the QAIC_c weights). Parameter estimates using model averaging suggested that both survival and recapture probabilities of female kestrels were lower among those with many fault bars compared to those with few fault bars (Table 2). For males, two models had the majority of support (Table 1). The most parsimonious model included an effect of fault bars on both survival and recapture probabilities ($\phi_g p_g$). The second-best model included an effect of fault bars on recapture probabilities only (ϕp_g). These models together received 74% of the support (Table 1). As predicted, parameter estimation using model averaging suggested that male kestrels with many fault bars were less likely to be recaptured on our study area in years following initial release (Table 2); however, in contrast to the results for females, it appeared that males with many fault bars may have had slightly higher survival probabilities compared to those with few fault bars, although the error associated with the estimate of survival for males with many fault bars was large (Table 2).

Discussion

POPULATION AND SEX DIFFERENCES

The majority of birds in our population (91.5%) had some fault bars on their primaries and rectrices. Smallwood (1989) reported that only 53% of 110 kestrels wintering in Florida had fault bars (apparently including secondary feathers as well). The lower proportion may be the result of methodological differences, or more plausibly real population differences. The birds wintering in Florida have completed their moult by the time they arrive (Smallwood 1989). In contrast, our birds winter in southern Mexico and Central America (G. R. Bortolotti, unpublished data) and are still moulting some feathers, especially their tails, during migration. The rigours of migration may thus be recorded as stressful events.

Male and female American kestrels have somewhat different moult schedules, and this in turn has been hypothesized as being responsible for sex differences in the timing of migration (Smallwood 1989). Females typically migrate before males (Mueller *et al.* 2000). In

Table 2. Model averaged estimates (\pm SE) of survival and recapture of male and female American kestrels according to whether their remiges and rectrices had few or many fault bars. See Methods for further details

Sex	Survival		Recapture	
	Few fault bars	Many fault bars	Few fault bars	Many fault bars
Females	0.42 \pm 0.03	0.33 \pm 0.05	0.25 \pm 0.04	0.17 \pm 0.04
Males	0.44 \pm 0.05	0.56 \pm 0.10	0.27 \pm 0.05	0.12 \pm 0.04

our study females had more fault bars. It seems unlikely that earlier migration is more stressful to birds; instead, migration may be inherently more difficult for females. There are, of course, many differences between the sexes that may explain the fault bars, but other lines of evidence also suggest that female kestrels are more prone to stress.

Kestrels, like most raptors, are sexually dimorphic in size (Bird 1988). As females are larger, they may have more difficulty obtaining sufficient energy for maintenance. The sexes also differ substantially in the roles in parental care. Dawson (1999) found that in our study area, breeding females supplemented with food during brood rearing subsequently had a higher return rate and so perhaps better survivorship (see below). Supplemented females, but not their mates, also reduced their foraging effort for their brood. Negative consequences of natural handicaps are also sex-specific, with females showing more detrimental effects than males (Dawson, Bortolotti & Murza 2001).

COMPONENTS OF FITNESS

How early eggs are laid in a season is one of the most important determinants of reproductive success and fitness in birds (e.g. Svensson 1997; Visser & Verboven 1999). Despite being able to arrive on the breeding grounds at the same time, it was clear that kestrels with many fault bars had delayed clutch initiation dates (Fig. 3). This may be the result of the birds' poorer condition (Fig. 1); they may simply have not been able to acquire sufficient nutrient reserves to breed. As the abundance of prey on territories did not vary with fault-bar category, birds with many fault bars may have been inferior foragers. Alternatively, given assortative mating, the poor quality individuals may have taken longer to acquire mates. It appears that the quality of both sexes was important for clutch initiation (Fig. 4) as might be expected, given that females are heavily, but not totally, dependent on their mates for food in the prelaying period (Bird 1988; personal observation). Although clutch size was not related independently to fault bars, birds with many fault bars laid fewer eggs because they laid late in the season.

That fault bars may play a role in mate choice is an interesting possibility. The positive association between members of a mated pair is not the product of two birds experiencing the same stressors in the previous year's breeding attempt; kestrels acquire new mates each year (G. R. Bortolotti, unpublished data). Most fault bars are obvious to us even at a distance beyond arm's length, so they could provide birds with an easy means of assessing prospective mates rapidly. Whether kestrels would use fault bars *per se*, or an alternative measure of condition (Bortolotti & Iko 1992), is unknown. However, Fitzpatrick & Price (1997) have speculated that fault bars could be a mechanism for honest signalling of reproductive potential. In their study of the black-billed magpie (*Pica pica*), Fitzpatrick

& Price (1997) found that damage to tails was important in mate choice and useful as a predictor of the number of offspring fledged. As fault bars weaken feathers, and as our study suggests that fault bars are indeed a predictor of quality, then damaged feathers are a sign that a bird is susceptible to stress.

Although various results presented here suggest a link between fault bars and quality of bird, they do not suggest causality. Except for the occasional breakage of feathers, it should not be costly physically to bear fault bars. Only 7% of kestrels in this study had broken flight feathers (Dawson *et al.* 2001). It is also unlikely, given the negative results of the blood analyses, that the stressful events that caused the bars had such long-lasting effects as to impair breeding performance. Instead, we suggest that the degree of fault-barring is an attribute of an individual, i.e. its susceptibility to stress. The percentages of feathers with fault bars were consistent from year to year (Fig. 2). It does not seem that increasing age or experience alleviates the negative effects of the myriad of causal agents that induce fault bars (Fig. 2).

In years following initial banding, we were more likely to recapture kestrels with few fault bars than many fault bars (Table 2). These results are in accordance with our previous analyses that suggested birds with many fault bars were less likely to breed; much of our data on recaptures come from birds trapped on nests during incubation. Although an intense amount of effort was invested in capturing birds on our study area each year, our recapture rates were generally low (Table 2). Because of this intensive trapping effort, we believe that relatively few birds went undetected on our area in any given year. We therefore suspect that the low recapture rates of kestrels, and even lower rates for those with many fault bars, may be the result of some birds not returning to our study area in every year they were alive (i.e. temporary emigration). Limited evidence from band recoveries supports this argument (G. R. Bortolotti, unpublished data). Temporary emigration would still represent a cost to fitness for birds with many fault bars because dispersing birds may have difficulty securing a breeding site and mate, and may breed less successfully at a new site (Boulinier *et al.* 1997; Bensch *et al.* 1998).

Perhaps the most important result in terms of impact on potential fitness was that female kestrels with many fault bars had a lower probability of survival (Table 2). In contrast, we found the opposite pattern in males; those with many fault bars apparently had higher survival. The error associated with the estimate of survival for males with many fault bars is large and so given the high degree of variation, we have little confidence that these represent real differences in survival. Regardless, the best model still suggested an effect of fault bars on survival (Table 1), and the direction is opposite to what we predicted. Because males with many fault bars appeared less likely to breed (above), these birds may not be subjected to the costs of reproduction and so

compared to males with few fault bars that did breed, had higher survival rates (e.g. Arnold & Clark 1996).

FUTURE CONSIDERATIONS

Why some kestrels should be more prone to suffer from stress than others is not known; however, both genetic and environmental effects during ontogeny are plausible. Tella *et al.* (2000b) found immunocompetence of fledgling American kestrels was largely a product of environment rather than genetics, and Tella *et al.* (2000a) found that variation in immunocompetence mimicked variation in return rates to our study area. This importance of rearing conditions could extend to susceptibility to stress, i.e. fault-bar formation. Studies linking stress and immunocompetence, both mechanistically and conceptually (e.g. Griffin 1989; Buchanan 2000), have a long history and it is not implausible that therein lies some explanation for our results. While fault bars are easy to evaluate, and feathers easy to obtain from living or dead birds, grappling with the complexity of the concepts of 'stress' and individual 'quality' will remain a challenge.

Whatever the causal agent and whatever the consequences may be, the use of fault bars show promise in addressing both proximate and ultimate questions in the biology of birds. As a research tool it is inexpensive and easy to evaluate, and is minimally intrusive and non-destructive. Individuals and populations can be re-evaluated over time, including the use of museum collections, and so fault bars may provide a means of monitoring environmental as well as individual health, as has been proposed for sexually selected traits (Hill 1995).

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