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Sex-dependent frequency and consequences of natural handicaps in American Kestrels

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Natural selection theory suggests that there should be fitness consequences for animals that possess morphological abnormalities such as missing or deformed appendages and other structures. As these characters are expected to be detrimental, morphological abnormalities could be considered “handicaps”. However, little information exists about the nature, prevalence or consequences of naturally occurring handicaps in birds, even though experimental handicapping has been used in some behavioural studies. Here, we document and describe the frequency of natural handicaps in American Kestrels *Falco sparverius*, and investigate their influence on condition and survival. We considered three different categories of handicap that should negatively impact falcons: missing remiges and rectrices, broken remiges and rectrices, and foot handicaps. Broken feathers, followed by missing feathers, were the most common handicaps detected in kestrels and their prevalence increased throughout the breeding season. Foot handicaps were relatively rare and showed no seasonal trends. There was no effect of any handicap type on body condition or return rates of male kestrels. In contrast, females with either foot handicaps or broken feathers were in significantly poorer condition than control females, and females with broken feathers were less likely than control females to return to the study area in years following initial capture. Given that female kestrels with broken feathers have more fault bars than those without broken feathers, and fault bar formation is related to stresses in a bird’s past, we suggest that female kestrels that had broken feathers were of poorer quality than those without broken feathers or those with missing feathers. Females with broken feathers may therefore have been in poorer condition initially than other birds, or if broken feathers are indicative of poor quality, then females with broken feathers may have been less able to cope with the negative impacts of feather loss on flight performance compared to birds with missing feathers.

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Animals vary naturally in their morphology, and the theory of natural selection suggests that those showing even subtle departures from optimal morphology should be at a selective disadvantage. Major departures from optimal morphology, such as missing or deformed appendages, are expected to be highly detrimental to animals that possess them and could thus be considered “handicaps”. But despite their potential importance in determining both survival and condition of animals, the nature, prevalence and consequences of these naturally occurring handicaps have received little attention. Some researchers investigating factors affecting bi-parental care in birds have manipulated work rates using experimental handicapping. Such methods have typically involved clipping a number of feathers or attaching weights to one member of a pair (Sanz et al. 2000 and references therein). The overall goal of these studies has been to increase the cost of parental care for one sex, and document the behavioural response of its partner. Handicapping has also figured prominently in some studies of sexual selection, where feathers have been experimentally altered (Møller and de Lope 1994). Despite the use of handicapping as an experimental technique, the effect of handicaps on individual birds generally has not been investigated. Similarly, some environmental pollutants such as polychlorinated biphenyls and heavy metals are known to cause morphological handicaps (Eeva and Lehikoinen 1996, Hoffman et al. 1998), but the consequences of these handicaps are also generally unknown.

Here, we document and describe the prevalence of naturally occurring handicaps in a wild population of the American Kestrel *Falco sparverius*, a small monogamous falcon, and investigate the association between these handicaps and the bird's condition and survival. Missing or broken feathers are known to have detrimental effects on flight performance, reducing both the ability of birds to capture prey and evade predators (Swaddle and Witter 1998). Many raptors likely kill their prey by squeezing with their toes, and talons are important for capturing, subduing and pinning prey to the ground (Csermely et al. 1991, Csermely and Gaibani 1998). Given the importance of both feather and foot attributes to successful foraging by falcons (Cade 1982), we predicted that birds with naturally occurring handicaps would be in poorer condition and have reduced survival compared to birds without such handicaps.

Methods

From 1990 to 1997, we studied American Kestrels breeding in nest boxes in the boreal forest near Besnard Lake in northern Saskatchewan, Canada (55°N, 106°W). Nest boxes were made available along approximately 200 km of road in a variety of habitats, ranging from densely forested areas to nearly treeless clearcuts (Bortolotti 1994), and 150 to 200 pairs bred in them annually (Tella et al. 2000). Kestrels arrived on our study area in mid- to late-April after migration, and began laying eggs in mid-May. We captured kestrels prior to laying using bal-chatri traps (Berger and Mueller 1959), and during incubation by hand in nest boxes.

Upon capture, each bird was banded with a unique combination of one aluminium and three coloured plastic leg bands. We inspected each bird for physical abnormalities and any with broken, missing or deformed talons or toes, or broken and missing remiges or rectrices, were classified as handicapped. No birds were found to have bill abnormalities. We grouped handicapped birds into three different categories: missing remiges or rectrices, broken remiges or rectrices, and foot handicaps. Individuals without such anomalies were used as controls. Kestrels began moulting during mid- to late-incubation and we captured most birds prior to the onset of moult; however birds that had missing feathers because of naturally occurring moult were not considered to be handicapped.

From 1993 to 1997, each bird was weighed (nearest g), and six linear measurements of size were taken: lengths of the exposed culmen, unflattened wing chord, tenth primary, inner and outer rectrices; and width of the tarsus at its narrowest point. These linear measures were entered into a principal components analysis, and the first component (PC1) was used as a measure of structural size. Separate analyses were performed for each sex (see Dawson and Bortolotti 1997 for details). Mass of an animal is partly a function of its structural size, so to obtain an index of body condition it is necessary to control for body size. Linear regressions with PC1 as the independent variable and body mass as the dependent variable were performed for males ($r = 0.31$, $F_{1,198} = 20.8$, $P < 0.001$) and females ($r = 0.17$, $F_{1,309} = 9.1$, $P < 0.01$) separately, and residuals were used as an estimate of body condition.

We tested whether there were sex differences in the frequency of handicaps using G tests, and whether the number of broken or missing feathers differed between the sexes using Mann-Whitney U tests. Seasonal variation in the frequency of handicaps was investigated using logistic regressions, with the presence of each handicap (yes/no) as the binary dependent variable, and date of capture (1 = 1 January) and year as independent variables. We used Spearman's correlations to test for seasonal changes in the number of broken or missing feathers. A series of logistic regressions were used to test whether body size was related to the prevalence of each handicap type. In each analysis, presence of a particular handicap (yes/no) was the dependent variable, with body size (PC1) and year as independent variables.

To test for relationships between handicaps and body condition we limited the data set to incubating birds only. The body condition of female kestrels increases dramatically prior to egg laying (Dawson and Bortolotti 1997), probably due to formation of eggs; therefore, including prelaying birds in analyses might obscure significant relationships. We used analysis of variance (ANOVA) with handicap type and year as independent variables, and condition as the dependent variable. For females, the variable handicap type had four levels: control, broken feathers, missing feathers, and foot handicaps. However, handicap type had only three levels for males because there were too few males captured with foot handicaps to be included as a separate level. If condition varied significantly among handicap types in ANOVA, Dunnett's tests (Zar 1999) were used to determine which handicap type differed from control birds. For all analyses where year was included as an independent variable, if year did not contribute significantly to the statistical model, it was removed and the analyses were performed again.

We used return rates to test whether handicaps had consequences for survival of parents. Return rates are a function of survival, dispersal, and recapture probabilities (Boulinier et al. 1997), but here we assume that birds that did not return to the study area were dead (see Discussion). Return rates of kestrels banded from 1990 to 1996 were determined by recapturing birds on our study area from 1991 to 1997. Where sample sizes allowed, we tested whether return rates differed between handicapped and control birds using G tests, otherwise Fisher's exact tests were used.

Means are presented $\pm$ SE and analyses were performed using SPSS (Norušis 1993) and SAS (SAS Institute Inc. 1990). Although we predicted that handicaps would have detrimental effects on kestrels, we took a conservative approach and used two-tailed tests throughout.

Results

Patterns of handicaps

We examined 1972 American Kestrels for handicaps from 1990 to 1997. Of these, three birds were found to have multiple handicaps; because we were interested in the potential effect of each type of handicap separately, and because sample sizes were small, these birds were excluded from further analysis. The most common anomaly, detected in 7% of kestrels, was broken remiges or rectrices (Table 1). Of birds with broken feathers, most (65% of males; 75% of females) suffered from damaged rectrices as opposed to remiges, and relative few birds were missing both types of feather (7.5% of males; 6.5% of females). The severity of broken feathers ranged from cases where only the tips were broken to those where major portions of remiges or all rectrices were broken at their bases. More females than males had at least one feather broken ($G = 6.6$, $df = 1$, $P = 0.01$; Table 1), but among these birds, the number of broken feathers did not differ between the sexes ($U = 1619$, $P = 0.23$), with males averaging 1.9 ± 0.3 (range 1 to 12, $n = 39$) and females 2.7 ± 0.4 (range 1 to 18, $n = 96$) broken feathers. The probability of a bird being captured with broken feathers increased throughout the breeding season for both males (logistic regression, $\chi^2 = 11.9$, $df = 1$, $P < 0.001$) and females ($\chi^2 = 9.7$, $df = 1$, $P < 0.01$). However, we detected seasonal increases in the number of broken feathers in females ($r_s = 0.27$, $n = 94$, $P = 0.01$) but not in males ($r_s = 0.14$, $n = 39$, $P = 0.40$).

Table 1. Frequency of morphological handicaps of American Kestrels captured during the breeding season, 1990–1997, in northern Saskatchewan. Percentages are indicated in parentheses.

Handicap type	Males n = 780	Females n = 1189	Pooled n = 1969
Broken feathers	40 (5.1)	96 (8.1)	136 (6.9)
Missing feathers	20 (2.6)	36 (3.0)	56 (2.8)
Foot handicaps	8 (1.0)	17 (1.4)	25 (1.3)

The second most common handicap, detected in 3% of birds, was missing remiges or rectrices (Table 1). In most cases (85% of males, 92% of females), birds were missing rectrices as opposed to remiges, and only a single female was found to be missing both remiges and rectrices. The proportion of males with at least one missing feather was similar to the proportion of females ($G = 0.4$, $df = 1$, $P = 0.54$). For birds with at least one missing feather, there was no difference between males (2.0 ± 0.5, range 1 to 12, $n = 20$) and females (2.2 ± 0.4, range 1 to 12, $n = 36$) in the number of missing feathers ($U = 346$, $P = 0.78$). The probability of missing feathers being detected on a bird increased throughout the breeding season (males: $\chi^2 = 5.9$, $df = 1$, $P = 0.02$; females: $\chi^2 = 9.4$, $df = 1$, $P < 0.01$), but there were no seasonal changes in the number of missing feathers (males: $r_s = 0.10$, $n = 20$, $P = 0.67$; females: $r_s = 0.06$, $n = 36$, $P = 0.71$). We also captured two male and four female kestrels that had supernumerary remiges or rectrices; however, because of small sample sizes and the fact that how such anomalies affect flight performance is unknown, we did not consider these birds further in our analyses.

Missing toes, missing or deformed talons, and broken legs were detected in only a small number of birds (Table 1). In nearly all cases, these foot abnormalities had occurred some time in the past and were completely healed. There were no differences between the sexes in the presence of foot handicaps ($G = 0.6$, $df = 1$, $P = 0.43$), nor did the probability of capturing a bird with a foot handicap vary throughout the breeding season (males: $\chi^2 = 0.1$, $df = 1$, $P = 0.71$; females: $\chi^2 = 0.2$, $df = 1$, $P = 0.70$).

Handicaps and attributes of birds

Body size, estimated using PC1, of both sexes of kestrels was unrelated to the probability of a bird possessing any type of handicap (logistic regressions, all $P > 0.30$). During incubation, body condition of males was unrelated to handicap type ($F_{2,193} = 0.3$, $P = 0.73$), but there was significant annual variation in body condition ($F_{4,193} = 3.3$, $P = 0.01$). In contrast, there was significant variation in body condition of females according to handicap type ($F_{3,307} = 3.7$, $P = 0.01$; Fig. 1). Dunnett's tests revealed that females with broken feathers and females with foot handicaps were in significantly poorer condition than control females ($P < 0.05$ in both cases). When we considered only females with at least one broken feather, body condition tended to decline as the number of broken feathers increased ($r_s = -0.32$, $n = 35$, $P = 0.06$; Fig. 2).

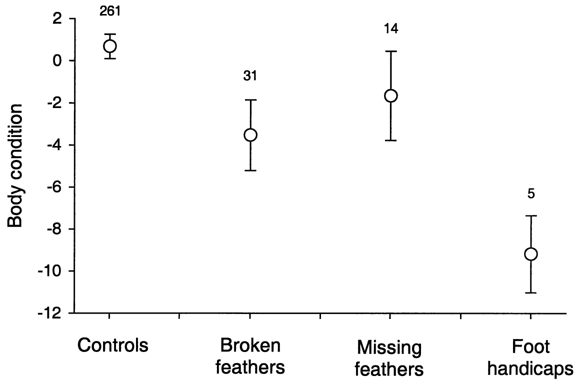

Fig. 1. Mean body condition ± SE during incubation of female American Kestrels in northern Saskatchewan according to handicap type. Control birds are those that possessed no handicaps. Condition was estimated using residuals from a linear regression between body mass and structural size (see Methods).

Broken feathers were associated with reduced survival of female kestrels, as females with at least one broken feather were less likely to return to the study area in years following capture than females without broken feathers (Table 2). Return rates of females with other handicap types did not differ from control females, and return rates of males were not related to presence or absence of handicaps (Table 2).

Discussion

Morphological handicaps that we detected in American Kestrels were similar to those identified in other species of birds, and in some cases occurred at similar frequencies. Although about 3–7% of kestrels had missing or broken feathers (Table 1), relatively few of these birds had damage to their wing feathers (1.9% or less).

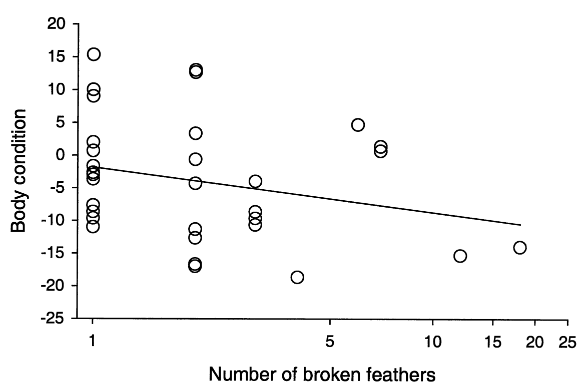

Fig. 2. Relationship between body condition of female American Kestrels during incubation and the number of broken feathers (remiges or rectrices) they possessed (P = 0.06). Number of broken feathers is plotted on a logarithmic scale. Condition was estimated using residuals from a linear regression between body mass and structural size (see Methods).

Table 2. Frequency of returning to the study area in northern Saskatchewan by American Kestrels in years subsequent to first capture, according to type of handicap. Data are for kestrels banded from 1990 to 1996, and recaptured between 1991 and 1997. Return rate of birds with each handicap type was compared to control birds that did not possess handicaps.

Sex	Handicap type	Return rate	P
Males	Controls	98/645 (15.2)	
	Broken feathers	6/38 (15.8)	0.92[a]
	Missing feathers	2/19 (10.5)	0.56
	Foot handicaps	0/7 (0.0)	0.60
Females	Controls	121/951 (12.7)	
	Broken feathers	1/79 (1.3)	<0.001[a]
	Missing feathers	2/29 (6.8)	0.57
	Foot handicaps	3/15 (20.0)	0.43

[a] G tests; all other P values are from Fisher's exact tests.

Similarly, studies of passerines have found wing anomalies in about 1.5% or fewer of birds (Hicks 1934, Sharp and Neill 1979, Post 1981). In contrast, foot handicaps occurred in about 1.3% of our kestrels, while foot anomalies in two species of blackbirds (Icteridae) were found in 2.5 to 3.2% of birds (Sharp and Neill 1979, Post 1981). In a study of wintering American Kestrels, Rogers and Dauber (1977) detected foot handicaps in 5% of birds. The difference between that study and ours may be related to the small sample of birds (n = 57) captured by Rogers and Dauber (1977).

We could not detect any differences in the proportion of females and males with missing feathers (Table 1), nor were there any sex differences in the number of missing feathers. Similarly, there were no sex differences in the proportion of birds with foot handicaps (Table 1). Both missing feathers and foot handicaps are likely the result of random accidents due to aggressive encounters with prey and predators, or from intraspecific conflicts. Although we expected sex differences in these two types of handicaps because the behaviour of male kestrels differs markedly from that of females during the breeding season (Balgooyen 1976, Dawson 1999), our results suggest that both sexes were exposed to similar injurious situations. In contrast, significantly more female than male kestrels had broken feathers (Table 1). Unlike missing feathers that are probably a random event, we suspect broken feathers are related to fault bars in feathers (see below). Fault bars are narrow, frayed bands in feathers resulting from abnormal or absent barbules (King and Murphy 1984), and feathers with fault bars are more likely to suffer breakage (Fitzpatrick and Price 1997). More frequent breakage of feathers in female kestrels is probably unrelated to the fact that females are larger than males, because within each sex the presence of broken feathers was unrelated to body size.

For both sexes of kestrel, the probability of encountering a bird with missing or broken feathers increased as the breeding season progressed. This seasonal increase in feather handicaps is probably related simply to the fact that birds captured later in the season had more time for feathers to become damaged or pulled out than birds captured early in the season. The number of broken feathers detected on females, but not on males, also increased significantly during the breeding season. Female kestrels enter and exit nest boxes far more frequently than males during breeding (Dawson 1999) and so would be more likely to incur feather damage as the season progresses. There were no seasonal changes in the number of missing feathers for either sex; this is not unexpected if missing feathers result from random processes (see above), as there is no reason to expect such processes that occurred early in the year would result in fewer feathers being pulled out compared to a process that occurred later.

The probability of a bird possessing a foot handicap did not vary with capture date. Although the same reasoning with regards to the seasonal increase in prevalence should apply to foot handicaps as feather handicaps, foot handicaps were relatively rare in our study compared to other handicaps (Table 1) and most were already healed. While our sample sizes were relatively large, they may have been inadequate to detect seasonal changes in frequencies of foot handicaps.

Female kestrels with broken feathers were in significantly poorer condition during incubation than control females (Fig. 1), and condition tended to decrease as the number of broken feathers increased (Fig. 2). Birds that have had feathers experimentally removed often lose mass, which may be an adaptive response to reduce flight costs (Swaddle and Witter 1997). This explanation seems unlikely for kestrels, because both missing and broken feathers are expected to have the same functional consequence in altering energetics of flight. If loss of mass, and hence condition, was a response for reducing flight costs, then we would also have expected to detect significant relationships between missing feathers and body condition. Moreover, we have previously shown that the presence of handicaps does not alter the predatory behaviour of female kestrels (Murza et al. 2000).

Fitzpatrick and Price (1997) speculated that feather damage is expected to correlate negatively with body condition if there is condition-dependent variation in feather strength. Female kestrels with broken feathers were in poorer condition (Fig. 1), and the number of broken feathers tended to correlate negatively with condition (Fig. 2). Given that female kestrels with broken feathers have more fault bars than those without broken feathers ($F_{1,1144} = 7.8$, $P < 0.01$; unpublished results), we suggest that female kestrels that had broken feathers were of poorer quality than those without broken feathers. Although the exact cause of fault bars is controversial (Negro et al. 1994), it is generally accepted that their formation is related to stress, often reductions in food intake (Machmer et al. 1992). However, we do not know whether broken feathers are a cause or a consequence of poor body condition of female kestrels. If poor quality birds were in poorer condition when feathers were initially grown, then these birds may have a higher incidence of fault barring, and hence broken feathers. Alternatively, if fault bars, and subsequently broken feathers, are indicative of poor quality birds, then females with broken feathers may have been less able to cope with the increased flight costs that are expected to arise from feather loss compared to birds that are missing feathers.

Support for the idea that female kestrels with broken feathers are of poor quality comes from the fact that they were less likely to return to the study area in years following banding than were control birds (Table 2). If females with broken feathers were of poorer quality, they may have been more susceptible to costs associated with feather loss, or may have suffered increased predation (Slagsvold and Dale 1996). However, we are unable to ascertain whether the cause of lower return rates of females with broken feathers is due to reduced survival because return rates are also a function of dispersal and recapture probability (Boulinier et al. 1997). Regardless, if these results are the product of differential dispersal, they may still represent costs because dispersing birds may have difficulty securing a breeding site and mate, and may breed less successfully at the new site (Boulinier et al. 1997, Bensch et al. 1998). Also, females with broken feathers may have returned at rates similar to control females but were not recaptured. Because we obtained a large proportion of return rate data by capturing kestrels during incubation, this might indicate that females with broken feathers were less likely to breed in subsequent years than control females. Reduced future fecundity of females may therefore be associated with the presence of broken feathers.

Female kestrels possessing foot handicaps were also in significantly poorer condition than control females during incubation, although foot anomalies were not associated with reduced return rates (Table 2). Small sample size probably limited the power of these tests to detect significant differences in return rates (Graves 1991). Kestrels in our population pair assortatively with respect to condition (Bortolotti and Iko 1992); because females are fed by their mates during incubation (Balgooyen 1976) our results may suggest that females with foot anomalies, and also those with broken feathers, may have been paired with poor quality males that were unable to supply sufficient food for females to maintain the same body condition as control females. Anecdotal evidence to support the idea that these females were paired with poor males comes from the fact that at one nest we never observed the male provisioning chicks, despite the fact that his mate had a fresh compound fracture of one of her legs and was feeding nestlings at a normal rate (R. D. Dawson, unpublished data). Additionally, if females with broken feathers had poor quality mates that provided little food, they may have been forced to hunt for themselves more frequently, and so been subjected to costs associated with altered energetics of flight that result from removal of feathers.

In conclusion, morphological handicaps were relatively common occurrences in American Kestrels breeding in northern Saskatchewan (Table 1), and in general had few deleterious effects on birds. The frequency of handicaps in most species of birds is generally unknown, owing to the paucity of reports in the literature. Among birds of prey, our own experience suggests that handicaps in species like Bald Eagles *Haliaeetus leucocephalus* are extremely rare (G. R. Bortolotti, pers. obs.). The ability of kestrels to cope with most handicaps is probably facilitated by the fact they utilize a diverse array of prey species, including small mammals, birds, reptiles, amphibians and insects (Balgooyen 1976; pers. obs.). Their adaptability to diverse habitats over a wide geographic range, extending from Alaska to Tierra del Fuego (Bird and Palmer 1988), may be of further benefit for individual kestrels that must overcome the potentially deleterious consequences of handicaps.

Our study has also shown that the presence of broken feathers of female American Kestrels is associated not only with reduced body condition, but also lower return rates to the study area in years following initial capture. We suggest that females with broken feathers are of poorer quality than control females. Given that broken feathers are associated with the presence of feather fault bars (see above), we concur with Negro et al. (1994) who suggested that feather condition may be indicative of the degree of stress that birds have encountered in the past, and may be useful indicators to compare stress levels both within and among populations. The sex-specific results that we found for the prevalence of broken feathers (Table 1), and the association with reduced body condition and return rates of females (Figs 1 and 2, Table 2), may indicate that female kestrels are subjected to greater stresses than males. Indeed, females have significantly more fault bars than males ($F_{1,1901} = 25.7$, $P < 0.001$; unpublished results). In addition, kestrels moult the majority of feathers during migration or even on the wintering areas (Balgooyen 1976), suggesting that much of this stress may occur after birds leave our study area. That female kestrels migrate farther than males, and occupy different winter habitats (Bird and Palmer 1988) may provide one possible explanation; however, further studies are needed to confirm these ideas.

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