

Plumage characteristics as an indicator of male parental quality in the American Kestrel

Jürgen Wiehn

Wiehn, J. 1997. Plumage characteristics as an indicator of male parental quality in the American Kestrel. – *J. Avian Biol.* 28: 47–55.

How females pair with respect to the plumage and provisioning characteristics of males, and its fitness consequences, was studied in the American Kestrel *Falco sparverius* in east central Pennsylvania, USA. Within a 100 km² area where pairing was studied, on the day females formed a pair bond they had approximately 3.4 unmated males to choose from. No male trait was clearly related to the time males had to wait before obtaining females. Indeed, the scarcity of unmated males together with extremely fast pairing (the pairs were usually formed within a day of males' arrival) suggest limited mating options for females. Male plumage brightness was related to age, adult males being brighter than yearlings. Early laying by females was associated with bright plumage of males, and high hatching success and food provisioning rate to nestlings were negatively correlated with the width of the subterminal band of yearling males. Males with bright plumage and a narrow subterminal tail band produced the most fledglings. This study indicates that plumage characteristics may reveal males' parental quality; plumage brightness predicts age and thus experience, and a narrow subterminal tail band predicts foraging ability especially of young, inexperienced males. Consequently, females mated to males with bright plumage color or with narrow subterminal tail band gain reproductive success. The results support the direct process of sexual selection, even though indirect processes may also exist.

J. Wiehn, Laboratory of Ecological Zoology, Department of Biology, University of Turku, FIN-20014 Turku, Finland. E-mail: jyrwie@sara.cc.utu.fi

A female may gain either direct benefits, which increase her own fitness in some way, or indirect benefits, which increase the fitness of her offspring, from the male (e.g. Kirkpatrick 1987, Kirkpatrick and Ryan 1991). Males may provide direct benefits to the female through territory and nest-site quality (Alatalo et al. 1986), or parental care (Searcy 1979, Yasukawa 1981). Males providing resources for their offspring or mate will benefit females by increasing female survival (Trivers 1972, Nur 1984) or reproductive output (Mock and Fujioka 1990). Several studies indicate that parenting abilities of males may be correlated with plumage color, females with brightly colored males thus gaining direct benefits (Grant and Grant 1987, Hill 1990, 1991, Norris 1990a, b, Palokangas et al. 1994, Sundberg and Larsson 1994, Sætre et al. 1995).

Indirect benefits are realized through the inheritance of "aesthetic" male traits (Weatherhead and Robertson

1979, 1981, Pomiankowski 1988), or good genes (Andersson 1982a, Kodrick-Brown and Brown 1984, Pomiankowski 1988, Grafen 1990a, b). Several studies have shown that females prefer extravagant male ornaments such as a long tail (e.g. Andersson 1982b, Møller 1988) or bright plumage (Hill 1991, Palokangas et al. 1994; for fishes see e.g. Endler 1983). Two hypotheses for the evolution of such a preference are the handicap (or good genes) model (Zahavi 1975, Hamilton and Zuk 1982, Isawa et al. 1991) and the runaway process (e.g. Pomiankowski et al. 1991). Recently, some evidence for indirect benefits through offspring has been found (Norris 1993, Petrie 1994).

The aim of this study is to investigate whether plumage characteristics of males could advertise parental quality in the American Kestrel *Falco sparverius*, a species in which the sexes differ dramatically in color. Further, the mating options of females,

how they pair with respect to male plumage and feeding characteristics and its fitness consequences are studied. In the American Kestrel, as in other raptors, it is mainly the provisioning effort of the male that contributes to the reproductive success of the pair (Balgooyen 1976, Bowman and Bird 1987). Therefore, females should try to acquire good quality males, and would clearly benefit if male quality could be evaluated quickly and accurately by plumage characteristics.

Methods

Study species

The American Kestrel is a monogamous, open-country, cavity-nesting raptor that readily uses nest-boxes. The male feeds the female after pair-formation, so that females hunt only infrequently before egg laying. The male provides for the whole family until the young are half grown (Balgooyen 1976). As in most diurnal raptors (Falconiformes) and owls (Strigiformes) (e.g. Andersson and Norberg 1981, Hakkarainen and Korpimäki 1991) the male is smaller than the female (reversed sexual size dimorphism). Intersexual differences in plumage coloration are also pronounced. The back of the male is rufous with black spots and the tail is rufous, with a black subterminal band. The upper wing coverts and some of the secondaries of the male are slate-blue, usually with black spots. Females are mostly reddish brown, with dark brown bars on the back and tail (Palmer 1988). Males vary considerably in their plumage pattern and coloration. The differences are most distinct in the brightness of the tail, wing and dorsal feathers, and in the width of the subterminal tail band.

Study area

American Kestrels were studied in east central Pennsylvania, USA, in the vicinity of Hawk Mountain Sanctuary (40°N, 75°W), in 1993. The total study area covered c. 800 km² and consisted of rolling farmland, hayfields and pastures broken up by small woodlands. The main crops in the area are corn *Zea mays*, soya-bean *Glycine max* and alfalfa *Medicago sativa*. Throughout the study area, kestrels breed in nest-boxes (210) fastened to isolated trees.

Arrival times and mating

A part (c. 100 km²) of the total study area was surveyed every other day between 20 March and 18 April to

determine when males arrived on their territories, and the time they formed pairs. Because the topography of the study area is rolling, this portion was chosen so that all parts could be observed equally well. As the area also contains kestrels which are winter residents (C. J. Robertson, unpubl. ringing data), only territories with arriving males were included in analyses of arrival and pairing (this let me leave one of 20 territories out). Arriving kestrels that were not color-ringed were identified by individual plumage characteristics to confirm that birds which arrived on territories stayed there. Furthermore, the time that it took males (19 in the 100 km² area) to mate after their arrival on the territories (mating lag) was determined. A male was considered as having mated once he was seen together with a female on his territory.

Behavioral observations

Behavioral data were collected by continuously recording (see Martin and Bateson 1986) the occurrence of different behavioral acts. I observed behavior using 10× binoculars and a wide angle, 20× telescope. To avoid disturbing the birds, recordings were made at a distance of 150–300 m from the nest. All observations were made on rainless days.

Usually within one week after the pairs were formed, and always before egg-laying, the behavior of 20 pairs was observed. The total time of observation was 6 hours per pair, divided into periods of 3 hours each in the morning and afternoon on different days. Likewise, during the mid-nestling period (when the young were 11–13 days old) 20 pairs were observed, for one 2.5 hour period each in the morning and afternoon on two different days. Based on these observations, the rate at which the male provisioned the female (in the courtship period) or female and young (in the nestling phase) was calculated for each male. In the nestling phase, a hunting efficiency index for males was calculated by dividing the feeding rate by the hunting effort (proportion of time spent actively hunting, i.e. directional flight between the nest and hunting area, flight bouts during hunting, and wind-hovering). The hunting effort of females during this phase also was recorded. Hunting from a perch, where falcons were observed to continually bob their heads and scan the surroundings, was included in the hunting effort of females, but not in that of males. In males, the intent was to examine the hunting yield per amount of time invested in an active hunting method requiring high energy expenditure (see Masman and Klaassen (1987) for energy requirements of different hunting methods), whereas for females, the intent was to determine only whether they devoted time to brooding or any kind of hunting.

Parental characteristics and reproductive success

The start of egg-laying was determined by regular visits to nest-boxes. During incubation, the boxes were checked to count the number of eggs. Nestlings were marked with U.S. Fish and Wildlife Service metal rings at the age of 2–3 weeks and nestlings which had survived were counted when they were 3–4 weeks old. After the young fledged, nest-boxes were checked for the remains of dead nestlings. Between 25 May and 20 July, males ($N = 57$) and females ($N = 58$) were trapped with a swing-door trap attached to the nest-box or with a bal-chatri when the nestlings were about one week old. Parent birds were marked with U.S. Fish and Wildlife Service metal ring and, in addition, with an individual combination of three plastic color-rings, for individual recognition. They were aged 1 (yearling) or >1 year old (adult) using the established criteria of Smallwood (1989), and their body mass determined with an accuracy of 1.0 g. Wing and tail lengths were measured to the nearest 1.0 mm, and tarsus length to the nearest 0.1 mm.

The colors of back, tail and wing feathers of trapped males were ranked into six categories, varying from 1 (dull) to 6 (bright). For ranking-criteria the Tikkurila Monicolor Nova paint color cards (Tikkurila Oy, Box 53, FIN-01301 Vantaa, Finland) and the color cards of Smithe (1975) were used. A male's tail and back are usually rufous, but vary from dull yellowish-brown to dark rufous. The color of the back and tail was ranked as 1 when yellowish-brown with rank numbers (2–6) increasing as the intensity of reddish color of the feathers increased. The ranking was based on the following Tikkurila paint color numbers (color card number(s) of Smithe (1975) in parentheses); 1 (yellowish-brown - dull): Y 162 B (39); 2: Y 135 C (37, 139); 3: Y 095 C (340, 38, 240); 4: Y 129 C (40, 136); 5: Y 089 C (32); 6 (dark rufous - bright): Y 130 C. The color of the wing (upper coverts and part of the secondary feathers) is usually slate-blue, and males were given a higher brightness rank with increasing intensity of blue. The ranking of wing feathers was based on the following color card numbers (Smithe (1975) in parentheses); 1: J 168 A; 2: K 168 C (84, 87); 3: N 168 C (83); 4: N 162 C; 5: L 162 C; 6: M 168 C. The ranking was repeated by an independent observer (C. J. Robertson). Back, tail and wing brightness of 57 males was intercorrelated (back-tail colors, Spearman rank correlation, $r_s = 0.47$, $p < 0.001$; back-wing, $r_s = 0.35$, $p = 0.009$; tail-wing, $r_s = 0.39$, $p = 0.003$). Therefore, an overall brightness score was determined by taking the mean of back, tail and wing brightness, and used in subsequent analyses. The width of the subterminal band on the third rectrix at the rachis was measured to the nearest 0.1 mm, using sliding calipers. Males were ranked and measured before their hunting and breeding success was known.

Statistics

Data were analyzed using SPSS for Windows (Norusis 1992) and SAS (SAS Institute Inc. 1990) statistical packages. The number of correlations calculated was 40 which means that c. two significant correlation coefficients should emerge just by chance. To correct significance levels for the correlations, I used the sequential Bonferroni procedure (Rice 1989) on a variable by table-wide level (e.g. in Table 1 arrival time, mating lag and laying date were handled as if they would have been in different tables). If a significance level is presented with Bonferroni correction, the term "corrected p " will be used. All statistical tests are two-tailed.

Results

Arrival times and pairing

Males arrived on breeding territories, on average, only one day before females, and the arrival times of the sexes did not differ significantly (males: median = 28 March, $N = 19$; females: median = 29 March, $N = 19$, Mann-Whitney U-test, $U = 163.0$, $p = 0.61$). There was a considerable overlap in arrival times of the sexes (Fig. 1). Pairs were usually formed within about one day (mean \pm SD = 1.1 ± 2.0 , $N = 19$) after a male had arrived on his territory, and 14 (out of 19) pairs were already formed when first observed. Each day a female arrived on a territory, there were about three (mean \pm SD = 3.4 ± 2.2 , $N = 19$) unmated males to choose from within the 100 km² study area.

Among the 58 trapped breeding females, 20 (35%) were yearlings (1 year old), whereas 24 of 57 (42%) of trapped breeding males were yearlings. Pair-formation was not assortative by age, i.e. neither yearling nor adult males paired with females of the same age more often than expected (Chi-square-test, $\chi^2 = 0.16$, $df = 1$, $p = 0.69$).

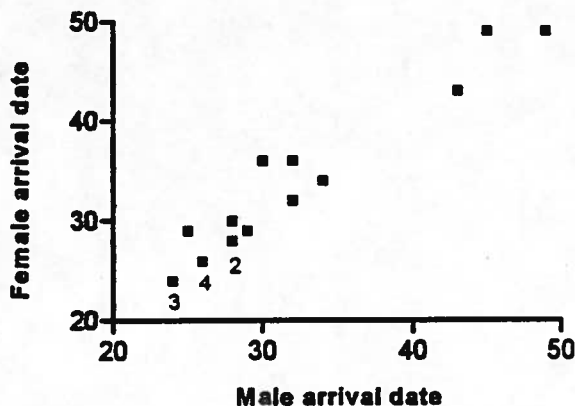


Fig. 1. Female arrival date in relation to male arrival date (1 = March 1). If more than one pair arrived on the same day, the number of pairs is given below the datapoint.

Table 1. Spearman rank correlations (r_s) between the plumage characteristics of American Kestrel males and their arrival time on territories, mating lag, and laying date of their partners. Significance levels are corrected by the sequential Bonferroni procedure (Rice 1989): °: corrected $p < 0.1$. *: corrected $p < 0.05$. **: corrected $p < 0.01$.

Male characteristics	Arrival of male r_s	Mating lag r_s	Laying date ² r_s	(N)
Brightness score ¹	-0.47	-0.11	-0.68* -0.56**	(15) (56)
Subterminal band width	0.18	0.54°	-0.05 -0.05	(14) (55)

¹ Brightness score was calculated as the mean score of back, tail and wing colors.

² Correlations between laying dates and male characteristics are given for both the males whose arrival times were determined (upper row) and for the whole study population (lower row).

Plumage characteristics of males were not closely associated with their arrival times (Table 1), nor was any measured body dimension (for example, tail length, Spearman rank correlation, $r_s = 0.11$, $N = 15$, $p = 0.7$). Females that paired early in the season had significantly longer tarsi than those that paired later in the season ($r_s = 0.76$, $N = 15$, corrected $p < 0.01$). The brightness score of males was correlated with the tarsus length of their females ($r_s = 0.34$, $N = 52$, corrected $p < 0.05$), but not with other measurements of females ($p > 0.1$).

In females, there were no age-related differences in arrival times on territories (mean arrival times, yearlings vs adults: 30 March vs 1 April, $U = 13.5$, $p = 0.94$). In males, there was a tendency for adults to arrive earlier than yearlings, although the difference was not significant (mean arrival times, yearlings vs adults: 5 April vs 29 March, $U = 11.0$, $p = 0.15$).

Females mated to brightly colored males began to lay eggs earlier than females with duller males (Table 1). The association between early laying and bright males also held after controlling for the effect of male arrival date in a partial correlation (Kendall partial rank correlation, $\tau = -0.44$, $N = 15$, corrected $p < 0.05$). Adult (>1-yr old) males had significantly higher brightness scores than yearling males (Table 2). Separate tests of the laying dates of females with yearling or adult males revealed that in both age classes, partners of brightly colored males started laying early in the season (Fig. 2).

Mating lag

The arrival date of the male did not correlate with the mating lag ($r_s = 0.21$, $N = 19$, $p = 0.39$). There was a weak, non-significant, negative correlation between the width of the subterminal band and the time males waited before obtaining a female (Table 1). In spite of

Table 2. Plumage characteristics of American Kestrel males as a function of age.

Male plumage characteristics	Male age		Mann-Whitney U-test	
	Yearling Mean \pm SD	Adult Mean \pm SD	U	p
Brightness score ¹	3.0 (0.8)	3.3 (0.9)	275.0	0.048
Subterminal band width (N)	25.3 (4.1) (24)	24.4 (2.9) (33)	341.0	0.44

¹ Brightness score as in Table 1.

a large sample size, the width of the subterminal band was not associated with tail length ($r_s = -0.11$, $N = 56$, $p = 0.43$), tail color ($r_s = -0.18$, $N = 56$, $p = 0.18$), or male age (Table 2).

There was a tendency, though not significant, for adult males to have shorter mating lags than yearling males (mean \pm SD, adults: 0.6 ± 1.3 ; yearlings: 2.5 ± 3.0 , $U = 13.5$, $p = 0.15$). For the males whose behavior I observed during courtship feeding, there were only two classes of mating lags (0 and 4 days). Males that paired the day they arrived on their territories tended to provide their partners with more prey items than those that mated four days after arriving (prey items/hour, mean \pm SD = 0.39 ± 0.2 vs 0.17 ± 0.0 , $U = 23.0$, $p = 0.075$). The arrival date of males did not correlate with

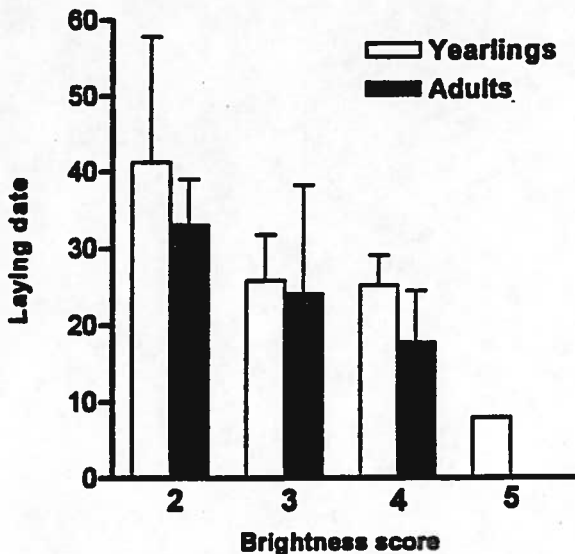


Fig. 2. Mean \pm SD laying date of females (1 = April 1) as a function of brightness score (mean score of back, wing and tail colours) of their partners (white bars: yearling males, Kruskal-Wallis test, $H = 9.61$, $p = 0.02$; black bars: adult males, $H = 10.01$, $p = 0.007$; age classes pooled, $H = 22.82$, $p < 0.0001$). No laying dates within any brightness score category differed significantly between yearling and adult males ($p > 0.05$). Number of cases (in increasing order of brightness scores): adult males: 6, 19, 7; yearling males: 12, 6, 5, 1.

Table 3. Spearman rank correlations (r_s) between the plumage characteristics of American Kestrel males and breeding performance of their partners. Significance levels are corrected by the sequential Bonferroni procedure (Rice 1989); *: corrected $p < 0.05$.

Male characteristics	Clutch size ²		Number of fledglings ¹	
	r_s	N	r_s	N
Brightness score ¹	0.25	57	0.35*	50
Subterminal band width	0.13	56	-0.29*	49

¹ Brightness score as in Table 1.

² Range 2-6 (mean \pm SD = 4.8 ± 0.6).

³ Range 0-6 (mean \pm SD = 3.9 ± 1.4).

their provisioning rate ($r_s = -0.13$, $N = 15$, $p = 0.65$), possibly suggesting that there were no obvious differences in food abundance (i.e. territory quality) between territories occupied early versus late. Males' plumage characteristics were not related to their courtship feeding rates ($p > 0.1$).

Reproductive success

Males with high brightness scores and males with a narrow subterminal tail band produced relatively large numbers of fledglings (Table 3); however, no such relationship was found with respect to clutch size (Table 3). The influence of males' provisioning on the clutch size could not be tested, since the provisioning data were from only two clutch size classes (4 and 5), and of the 20 pairs observed, only two had 4-egg clutches. Since both clutch size and the number of fledglings were correlated negatively with laying date ($r_s = -0.44$, $N = 60$, $p < 0.001$ and $r_s = -0.34$, $N = 52$, $p < 0.01$, respectively), the productivity was also tested when the effect of laying date was controlled for. With laying date as a covariate, the association of male plumage color with productivity disappeared ($\tau = 0.16$, $N = 50$, $p = 0.11$), whereas the negative correlation with the width of the subterminal tail band remained significant ($\tau = -0.20$, $N = 49$, $p = 0.04$). The age of the male was not associated with his reproductive success, as productivity did not differ between yearling and adult males (mean \pm SD, eggs: 4.8 ± 0.7 vs 4.8 ± 0.6 , $U = 386.5$, $p = 0.81$; and fledglings: 3.8 ± 1.5 vs 4.0 ± 1.4 , $U = 256.5$, $p = 0.36$).

In 25% of the clutches some of the eggs did not hatch (range of unhatched eggs 0-5, mean \pm SD = 0.5 ± 1.2 , $N = 56$). Plumage characteristics appeared to be associated with hatching success as the width of the subterminal band of young males correlated positively with the percentage of unhatched eggs in the clutch ($r_s = 0.43$, $N = 22$, $p < 0.05$), but not that of the adults ($r_s = 0.02$, $N = 30$, $p = 0.98$). In addition, the brightness score was

negatively, although only marginally, related to percentage of unhatched eggs in clutches of both yearling ($r_s = -0.36$, $N = 22$, $p = 0.097$) and adult ($r_s = -0.30$, $N = 31$, $p = 0.10$) males.

One explanation for the association between plumage and reproductive success may be that patterns of coloration are also related to provisioning rates of males. Young males with narrow subterminal bands had higher prey delivery rates during the nestling period than those with wider subterminal bands ($r_s = -0.85$, $N = 8$, $p < 0.01$), but in adult males there was no such relationship ($r_s = -0.19$, $N = 11$, $p = 0.59$). The hunting efficiency (number prey caught/percentage of time in flight hunting) of yearling males was also negatively related to the width of their subterminal band ($r_s = -0.81$, $N = 8$, $p < 0.05$), but in adult males there was, again, no similar tendency ($r_s = -0.11$, $N = 11$, $p = 0.74$). The brightness score was not clearly related to prey delivery rate in yearling ($r_s = 0.60$, $N = 8$, $p = 0.12$) or in adult males ($r_s = 0.25$, $N = 12$, $p = 0.87$). Differences in either the provisioning rate or hunting efficiency during the nestling phase were unrelated to male age per se ($U = 45.0$, $p = 0.81$, and $U = 46.0$, $p = 0.88$, respectively).

After controlling for brood size, partners of males with wide subterminal tail bands spent more time hunting than partners of males with narrow subterminal bands (Fig. 3). No other traits of males were associated with the time females hunted. When laying date was controlled for, there was no relationship between the proportion of time females spent in hunting during the mid-nestling phase and the number of fledglings produced by the pair ($\tau = -0.14$, $N = 20$, $p = 0.16$).

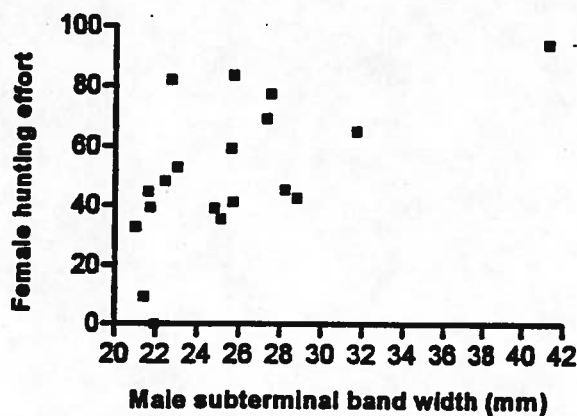


Fig. 3. Hunting effort of female American Kestrels (proportion of time used in perch-hunting and flight-hunting) during the mid-nestling phase in relation to the width of the subterminal band on the tail of their males (Kendall partial rank correlation, controlling for brood size, $\tau = 0.39$, $N = 19$, $p < 0.05$). If the male with the widest band is excluded, the correlation still remains significant ($\tau = 0.35$, $N = 18$, $p < 0.05$).

Discussion

Arrival and mating

Male American Kestrels in my study area obtained females soon after arriving on territories, usually within one day. An earlier study at the same site showed that new pairs form each year (Apanius 1991). Within the 100 km² area where pairing was studied, female kestrels appeared to have, on average, 3.4 mating options upon arrival. Can females be choosy given that the pairing is so fast and available males so scarce? In the Great Reed Warbler *Acrocephalus arundinaceus* (Bensch and Hasselquist 1992) and the Pied Flycatcher *Ficedula hypoleuca* (Dale et al. 1992) females search for mates within a radius of only a few hundred meters once they have located an available male, but search patterns have not been studied in any bird of prey, to my knowledge. However, it seems likely that female kestrels could search an area much larger than do small passerines, especially as the typical summer habitat of these falcons is an open landscape which probably enables females to locate males flying even a few kilometers away. Even so, the number of available males may be too small for females to be choosy. Time and energy constraints for females while choosing mates are well demonstrated (e.g. Parker 1983, Alatalo et al. 1988, Slagsvold et al. 1988, Real 1990, Palokangas et al. 1992, Sullivan 1994). If females visit and assess many males, the males visited earlier may simply be paired with newly-arrived females when they return to them (e.g. Real 1990). Another severe constraint for both sexes is the fact that in temperate areas prospects for breeding decline rapidly as the season progresses (e.g. Village 1985, Palokangas et al. 1992, this study). Therefore, female American Kestrels may not have high criteria for mates, and their best option may be to choose the first male encountered.

Bortolotti and Iko (1992) found that in wild American Kestrels mating was assortative by condition, whereas a study of captive American Kestrels indicated the importance of frequent nest-site inspections by males in mate choice situations (Duncan and Bird 1989). In this study, no male trait was clearly related to the time males remained unpaired after arriving on their territories (mating lag); this was possibly because of the scarcity of unpaired males, and the fact that there was very little variation in the mating lags (most pairs were formed within a day of the male's arrival; Fig. 1). Two tendencies, however, emerged: males with high rates of courtship feeding and with narrow subterminal bands seemed to pair slightly faster than those with low feeding rates and wide bands. Although the plumage characteristics I measured were not strongly related to pairing, the effects of color patterns invisible to the human eye (e.g. Bennett et al. 1994) cannot be ruled out as a cue for female mate choice. Experiments

in Eurasian Kestrels *Falco tinnunculus* have demonstrated the importance of ultraviolet vision in finding patches of high vole abundance (Viitala et al. 1995). In addition, females might be choosing males based on some other trait, e.g. nest-site quality, correlated with male color. Indeed, isolating criteria for mate choice is extremely difficult because of many confounding variables (see Andersson 1994).

Fitness and male traits

The secondary sexual traits of a male were associated with the number of fledglings he raised: brightly colored males and males with narrow subterminal bands were the most productive (Table 3). Females mated to brightly colored males likely had higher fitness because they initiated egg-laying early. The association between early laying and bright male plumage color occurred in both adult and yearling males (Fig. 2). Color may be an indicator of the ability of these males to get their females into laying condition quickly. Alternatively, high quality females mate with bright males, or females mated with bright males invest more in breeding than those mated with dull males, as suggested by the differential allocation hypothesis (Burley 1988). As the plumage traits of males were not related to their rate of courtship feeding, it may be that brightly colored males were paired with good quality females, able to start laying early. As most of the pairs were already formed when first observed, it cannot be ruled out that the brightly colored males formed pairs before arriving on territories. Interestingly, females with brightly colored males had long tarsi, possibly indicating female-female competition for the bright males.

Unlike the case with plumage color, the laying date of females was not related to the width of the subterminal tail band of their males. Still, males with narrow subterminal bands had large broods at the time of fledging. A narrow tail band of yearling males was associated with a high provisioning rate to nestlings. Furthermore, hatching failures of eggs within clutches were infrequent for males with narrow subterminal bands, and females mated to males with narrow subterminal bands had little need to hunt during the mid-nestling phase (Fig. 3). The reasons for hatching failures are unknown, but perhaps some component of the viability of eggs is related to the quality of the parents: females can vary in their fertility and males can vary in their ability to fertilize the eggs (e.g. Birkhead and Moller 1992). Plumage characteristics of males may, for example, be related to the quality or quantity of their sperm. Whatever proximate mechanism is involved, these results suggest that females and nestlings of males with narrow tail bands received adequate provisioning from the male. In American Kestrels, as in other raptors, it is mainly the effort of the male that

determines the reproductive success of the pair (Balgooyen 1976, Bowman and Bird 1987).

It is generally believed that the expression of secondary sexual traits varies according to the condition of the individual (Andersson 1982a). In the House Finch *Carpodacus mexicanus*, the amount of red in the plumage of males is a function of dietary intake of carotenoids (Brush and Power 1976, Ralph 1969 for other birds). The brightness of the plumage is then used as a cue for female mate choice, and is correlated with male parental quality (Hill 1990, 1991). In American Kestrels, adult (> 1-yr old) males had brighter plumage than yearling males (Table 2); therefore, plumage color may be an honest advertisement of male quality and experience. This gives the female the opportunity to discriminate between inexperienced and experienced males. In many other falcon species, including the Eurasian Kestrel, age discrimination among males is facilitated by the female-like plumage of yearlings (e.g. Village 1990, Hakkarainen et al. 1993).

Plumage brightness varied within, as well as between, age classes of males. Differences among individuals may be related to factors at the time of molt. American Kestrels molt their flight and body feathers annually, before autumn migration (Palmer 1988). Therefore, the quality of feathers which the adults produce is potentially affected by the condition during the previous breeding attempt, and thus only the least stressed males may be able to produce showy feathers. In juveniles, feathers are produced during the nestling and fledgling periods, and feather quality is probably most affected by the food received from parents. Compared to color, it is difficult to explain the narrow subterminal band as either a genetic- or nutrition-based indicator of male quality, especially since females are usually thought to prefer exaggerated, not reduced, size or color of traits (see Enquist and Arak 1993). Either it must be costly to produce a narrow subterminal band, the tail band is related to some other trait, or the relationship between this trait and viability is spurious. One possible cost could be to produce a wide rufous area on the tail. Based on allometry, the width of the subterminal band should be correlated with tail length, but this was not true. Therefore, the physiological cost of producing tail colors could be linked to producing a wide rufous area of the tail, rather than to producing a narrow subterminal band. Whatever mechanisms are involved, it appears that plumage characteristics indicate whether or not a male will be a good parent. For females this may be of crucial importance especially when choosing among yearling males, which are usually thought to be less skilled than adults (Lack 1966, Curio 1983, Sætre et al. 1995). Females mating with showy males may obtain a vigorous mate who is in good condition and is a skilful hunter. Such direct benefits to females are predicted by the "good parent" process of sexual selection (Heywood 1989, Hoelzer 1989, Price et al. 1993) and

have been found in other studies too (e.g. Hill 1990, 1991, Palokangas et al. 1994, Sundberg and Larsson 1994).

In conclusion, these results suggest that female American Kestrels may be able to predict male parental quality from his external traits. Bright plumage and narrow subterminal tailbands appear to be reliable cues so that females mated with such males gain reproductive success. However, the degree to which females can be choosy depends on the number of mating options and on the time and energy constraints of searching. Given the low density of males and the short breeding season the best option for females in this study may have been to mate with the first available male.

Acknowledgements - I thank Erkki Korpimäki and Jorma Sorjonen for supervising the study, and Rauno V. Alatalo, Keith L. Bildstein, Gary R. Bortolotti, Harri Hakkarainen, Jan T. Liffeld, Kai Norrdahl, Glenn-Peter Sætre, Karen L. Wiebe, and an anonymous referee for constructive comments on the manuscript. I am also grateful to the staff of Hawk Mountain Sanctuary, especially Keith L. Bildstein, James Brett and Laurie J. Goodrich, for their help and encouragement during the work. For assisting in the field I want to thank Jim Klucsarits and especially Bob and Sue Robertson, who did not spare any time and energy when helping me. In addition, I was assisted by the Hawk Mountain Sanctuary 1993 Interns, especially Flor E. Galán Amaro. The field work was supported financially by the Hawk Mountain Sanctuary Internship and the Hawk Mountain Sanctuary-Zeiss Research Award. In the final phase, I was supported by the Emil Aaltonen Foundation. This is Hawk Mountain Sanctuary contribution number 46.

References

- Alatalo, R. V., Carlson, A. and Lundberg, A. 1988. The search cost in mate choice of the pied flycatcher. - *Anim. Behav.* 36: 289-291.
- , Lundberg, A. and Glynn, C. 1986. Female pied flycatchers choose territory quality and not male characteristics. - *Nature* 323: 152-153.
- Andersson, M. 1982a. Sexual selection, natural selection and quality advertisement. - *Biol. J. Linn. Soc.* 17: 375-393.
- 1982b. Female choice selects for extreme tail length in a widowbird. - *Nature* 299: 818-820.
- 1994. Sexual selection. - Princeton University Press, Princeton.
- and Norberg, R. Å. 1981. Evolution of reversed sexual size dimorphism and role partitioning among predatory birds, with size scaling of flight performance. - *Biol. J. Linn. Soc.* 15: 105-130.
- Apanius, V. 1991. Blood parasitism, immunity and reproduction in American kestrels (*Falco sparverius* L.) - PhD dissertation, University of Pennsylvania, Philadelphia.
- Balgooyen, T. G. 1976. Behaviour and ecology of the American kestrel (*Falco sparverius*) in the Sierra Nevada of California. - *Univ. Calif. Publ. Zool.* 103: 1-83.
- Bennett, A. T. D., Cuthill, I. C. and Norris, K. J. 1994. Sexual selection and the mismeasure of color. - *Am. Nat.* 144: 848-860.
- Bensch, S. and Hasselquist, D. 1992. Evidence for active female choice in a polygynous warbler. - *Anim. Behav.* 44: 301-311.
- Birkhead, T. R. and Møller, A. P. 1992. Sperm competition in birds. Evolutionary causes and consequences. - Academic Press, London.

- Bortolotti, G. R. and Iko, W. M. 1992. Non-random pairing in American kestrels: mate choice versus intra-sexual competition. - *Anim. Behav.* 44: 811-821.
- Bowman, R. and Bird, D. M. 1987. Behavioral strategies of American kestrels during mate replacement. - *Behav. Ecol. Sociobiol.* 20: 129-135.
- Brush, A. H. and Power, D. M. 1976. House finch pigmentation: carotenoid metabolism and the effect of diet. - *Auk* 93: 725-739.
- Burley, N. 1988. The differential-allocation hypothesis: an experimental test. - *Am. Nat.* 132: 611-628.
- Curo, E. 1983. Why do young birds reproduce less well? - *Ibis* 125: 400-404.
- Dale, S., Rinden, H. and Slagsvold, T. 1992. Competition for a mate restricts mate search of female pied flycatchers. - *Behav. Ecol. Sociobiol.* 30: 165-176.
- Duncan, J. R. and Bird, D. M. 1989. The influence of relatedness and display effort on the mate choice of captive female American kestrels. - *Anim. Behav.* 37: 112-117.
- Endler, J. A. 1983. Natural and sexual selection on color patterns in poeciliid fishes. - *Envir. Biol. Fishes* 9: 173-190.
- Enquist, M. and Arak, A. 1993. Selection of exaggerated male traits by female aesthetic senses. - *Nature* 361: 446-448.
- Grafen, A. 1990a. Sexual selection unhandicapped by the Fisher process. - *J. theor. Biol.* 144: 473-516.
- 1990b. Biological signals as handicaps. - *J. theor. Biol.* 144: 517-546.
- Grant, B. R. and Grant, P. R. 1987. Mate choice in Darwin's finches. - *Biol. J. Linn. Soc.* 32: 247-270.
- Hakkarainen, H. and Korpimäki, E. 1991. Reversed sexual size dimorphism in Tengmalm's Owl: is small male size adaptive? - *Oikos* 61: 337-346.
- , Korpimäki, E., Huhta, E. and Palokangas, P. 1993. Delayed maturation in plumage colour: evidence for the female-mimicry hypothesis in the kestrel. - *Behav. Ecol. Sociobiol.* 33: 247-251.
- Hamilton, W. D. and Zuk, M. 1982. Heritable true fitness and bright birds: a role for parasites? - *Science* 218: 384-387.
- Heywood, J. S. 1989. Sexual selection by the handicap mechanism. - *Evolution* 43: 1387-1397.
- Hill, G. E. 1990. Female house finches prefer colourful males: sexual selection for a condition-dependent trait. - *Anim. Behav.* 40: 563-572.
- 1991. Plumage coloration is a sexually selected indicator of male quality. - *Nature* 350: 337-339.
- Hoelzer, G. A. 1989. The good parent process of sexual selection. - *Anim. Behav.* 38: 1067-1078.
- Isawa, Y., Pomiankowski, A. and Nee, S. 1991. The evolution of costly mate preferences. II. The 'handicap' principle. - *Evolution* 45: 1431-1443.
- Kirkpatrick, M. 1987. The evolutionary forces acting on female mating preferences in polygynous animals. - In: Bradbury, J. W. and Andersson, M. B. (eds.). *Sexual selection: testing the alternatives*. John Wiley, London, pp. 67-82.
- and Ryan, M. J. 1991. The evolution of mating preferences and the paradox of the lek. - *Nature* 350: 33-38.
- Kodrick-Brown, A. and Brown, J. H. 1988. Truth in advertising: the kinds of traits favored by sexual selection. - *Am. Nat.* 124: 309-323.
- Lack, D. 1966. *Population studies of birds*. - Clarendon Press, Oxford.
- Martin, P. and Bateson, P. 1986. *Measuring behaviour*. - Cambridge University Press, New York.
- Masman, D. and Klaassen, M. 1987. Energy expenditure during free flight in trained and free-living Eurasian kestrels (*Falco tinnunculus*). - *Auk* 104: 603-616.
- Mock, D. W. and Fujioka, M. 1990. Monogamy and long-term pair bonding in vertebrates. - *Trends Ecol. Evol.* 44: 39-43.
- Møller, A. P. 1988. Female choice selects for male sexual tail ornaments in the monogamous swallow. - *Nature* 332: 640-662.
- Norris, K. J. 1990a. Female choice and the evolution of the conspicuous plumage coloration of monogamous male great tits. - *Behav. Ecol. Sociobiol.* 26: 129-138.
- 1990b. Female choice and the quality of parental care in the great tit *Parus major*. - *Behav. Ecol. Sociobiol.* 27: 275-281.
- 1993. Heritable variation in a plumage indicator of viability in male great tits *Parus major*. - *Nature* 362: 537-539.
- Norusis, M. J. 1992. *SPSS for Windows: Base System User's Guide, Release 5.0*. - SPSS, Chicago.
- Nur, N. 1984. The consequence of brood size for breeding blue tits. I. Adult survival, weight change and the cost of reproduction. - *J. Anim. Ecol.* 53: 479-496.
- Palokangas, P., Alatalo, R. V. and Korpimäki, E. 1992. Female choice in the kestrel under different availability of mating options. - *Anim. Behav.* 43: 659-665.
- , Korpimäki, E., Hakkarainen, H., Huhta, E., Tolonen, P. and Alatalo, R. V. 1994. Female kestrels gain reproductive success by choosing brightly ornamented males. - *Anim. Behav.* 47: 443-448.
- Palmer, R. S. 1988. American kestrel. - In: Palmer, R. S. (ed.). *Handbook of North American birds*. Vol. 5. Yale University Press, Connecticut, pp. 253-290.
- Parker, G. A. 1983. Mate quality and mating decisions. - In: Bateson, P. (ed.). *Mate choice*. Cambridge University Press, Cambridge, pp. 141-166.
- Petrie, M. 1994. Improved growth and survival of offspring of peacocks with more elaborate trains. - *Nature* 371: 598-599.
- Pomiankowski, A. N. 1988. The evolution of female mate preferences for mate genetic quality. - In: Harvey, P. H. and Partridge, L. (eds.). *Oxford surveys in evolutionary biology*. Oxford University Press, Oxford, pp. 136-184.
- , Isawa, Y. and Nee, S. 1991. The evolution of costly preferences. I. Fisher and biased mutation. - *Evolution* 45: 1422-1431.
- Price, T. D., Schluter, D. and Heckman, N. E. 1993. Sexual selection when the female directly benefits. - *Biol. J. Linn.* 48: 187-211.
- Ralph, C. I. 1969. The control of color in birds. - *Amer. Zool.* 9: 521-530.
- Real, L. 1990. Search theory and mate choice. I. Models of single-sex discrimination. - *Am. Nat.* 136: 376-404.
- Rice, W. R. 1989. Analysing tables of statistical tests. - *Evolution* 43: 223-225.
- Sætre, G.-P., Fosnes, T. and Slagsvold, T. 1995. Food provisioning in the pied flycatcher: do females gain direct benefits by choosing bright-coloured males? - *J. Anim. Ecol.* 64: 21-30.
- SAS Institute Inc. 1990. *SAS/STAT User's Guide: Statistics, Version 6 Edition*. - SAS Institute Inc. Cary, DC.
- Searcy, W. A. 1979. Female choice of mates: A general model for birds and its application to red-winged blackbirds (*Agelaius phoeniceus*). - *Am. Nat.* 114: 77-100.
- Slagsvold, T., Lifjeld, J. T., Stenmark, G. and Breichagen, T. 1988. On the cost of searching for a mate in female pied flycatchers. *Ficedula hypoleuca*. - *Anim. Behav.* 36: 433-442.
- Smallwood, J. A. 1989. Age determination of American kestrels: a revised key. - *J. Field Ornithol.* 60: 510-519.
- Smithe, F. B. 1975. *Naturalists's color guide, Part I, the color guide*. - American Museum of Natural History, New York, New York.
- Sullivan, M. S. 1994. Mate choice as information gathering process under time constraint: implications for behaviour and signal design. - *Anim. Behav.* 47: 141-151.
- Sundberg, J. and Larsson, C. 1994. Male coloration as an indicator of parental quality in the yellowhammer, *Emberiza citrinella*. - *Anim. Behav.* 48: 885-892.
- Trivers, R. L. 1972. Parental investment and sexual selection. - In: Campbell, P. (ed.). *Sexual selection and the descent of man*. Aldine, Illinois, Chicago, pp. 136-179.

- Viitala, J., Korpimäki, E., Palokangas, P. and Kowala, M. 1995. Kestrels are attracted to vole scent marks visible in ultraviolet light. - *Nature* 373: 425-427.
- Village, A. 1985. Spring arrival times and assortative mating of kestrels in south Scotland. - *J. Anim. Ecol.* 54: 857-868.
- 1990. *The kestrel*. - Poyser, London.
- Weatherhead, P. and Robertson, R. J. 1979. Offspring quality and the polygyny threshold: "the sexy son hypothesis". - *Am. Nat.* 113: 201-208.
- 1981. In defence of the "sexy son hypothesis". - *Am. Nat.* 117: 349-356.
- Yasukawa, K. 1981. Male quality and female choice of mate in the red-winged blackbird (*Agelaius phoeniceus*). - *Ecology* 62: 922-929.
- Zahavi, A. 1975. Mate selection - a selection for a handicap. - *J. theor. Biol.* 53: 205-214.

(Received 7 March 1996, revised 14 August 1996, accepted 26 August 1996.)