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A test of male mating and hunting success in the kestrel: the advantages of smallness?

Abstract We tested female choice for male wing and tarsus length and body mass in the kestrel (*Falco tinnunculus*), a species in which males average about 10% smaller than females. We also studied how male characters are related to their hunting success. In the laboratory, females preferred lighter males with shorter tarsi as mates, if the difference in those characters between competing males was larger than average. Lighter and shorter-winged males seemed to be better hunters than heavier and longer-winged males. Field observations in a year in which voles were scarce suggested that shorter-winged males were also better food providers in courtship feeding than longer-winged males, although in good vole years such a relationship was not found. We argue that females may prefer to pair with smaller males, because they have higher flight performance and better hunting success than heavier males. By doing so, females may gain direct breeding advantages. We conclude that both female choosiness and the hunting efficiency of males well contribute to reversed sexual size dimorphism (RSD, females larger than males) in the kestrel.

Key words Mate choice · Body size · Reversed sexual size dimorphism · Hunting success · Raptor

Introduction

To date, sexual size dimorphism (SSD) has been the topic of several studies (e.g. Ralls 1977; Shine 1988;

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Hedrick and Temeles 1989; Fairbairn and Preziosi 1994), and plausible mechanisms causing SSD have been suggested ever since Darwin (1874). SSD is thought to be the product of natural or sexual selection, or both (e.g. Hedrick and Temeles 1989). Of these, sexual selection is most often emphasized. Variation in body size of males, for example, may result in fitness differences among males if mating success in inter-male competition is enhanced by large body size (e.g. Clutton-Brock and Iason 1986). The large size of males compared to females may thus result from intensive competition between males (intra-sexual selection) or female choosiness for large male body size (inter-sexual selection). In addition to sexual selection, reproductive role division and intersexual food competition between the sexes may also increase SSD (see Hedrick and Temeles 1989). Reproductive role devision is thought to result mostly from selection pressures acting on female fecundity (e.g. Ralls 1976; Wiklund and Karlsson 1988), whereas intersexual food competition results in selection on both sexes to reduce food niche overlap (Peters and Grubb 1983; Temeles 1986).

In raptors, as well in many other animals (Shine 1988), females are larger than males (reversed sexual size dimorphism, RSD). At least four hypotheses have been proposed to explain RSD in raptors. Two of these stress the importance of large female size in the evolution of RSD: (1) large females may produce more offspring and/or provide better parental care than small females (see e.g. Ralls 1976); (2) large females may be better at competing for good-quality males, especially important when parental effort of males is considerable (e.g. Trivers 1972; Petrie 1983; Newton 1986). The other two hypotheses instead focus on the significance of small male size in RSD: (3) females may choose small males as mates if female dominance over males enhances breeding success (Perdeck 1960); (4) selection may favour small male size if smallness is related to mating success or reproductive output (see

e.g. Balgooyen 1972; Earhart and Johnson 1970; Reynolds 1972).

Some evidence has been found for most RSD hypotheses in studies of other animals (for a review see Hedrick and Temeles 1989), but no clear consensus has yet emerged concerning the relative importance of these factors in the evolution of RSD among raptors (for reviews see Newton 1979; Andersson and Norberg 1981; Mueller and Meyer 1985; Temeles 1985; Jehl and Murray 1986; Hakkarainen and Korpimäki 1991). In most birds of prey, the female incubates and broods the young, while the male does most of the hunting (Newton 1979; Korpimäki 1981; Mikkola 1983). Therefore, the breeding female depends on male hunting and provisioning skills.

Hunting is costly in terms of energy expenditure, and this may explain why in the kestrel (*Falco tinnunculus*), for example, the energy expenditure of males in the breeding season is more than 30% greater than that of females (Masman et al. 1989). If smaller size increases the hunting efficiency of males (e.g. Balgooyen 1972; Hakkarainen and Korpimäki 1991), then strong intersexual selection on small male size can be expected, especially if there is variation in male hunting efficiency and their contribution to breeding success. As a result, females should choose males with the highest hunting efficiency. In general, because males' investment in hunting and breeding is high, both the benefits and costs for the female when choosing a male increase with the level of male investment. Therefore, hunting success is probably an important selection criterion for the choosing female, as the fitness of female is mostly determined by the male's ability to provide food during most breeding seasons (Village 1990; Palokangas et al. 1992; Wiehn 1997). Previous studies have shown that female raptors may also use other direct cues in mate choice, like male display activity (Simmons 1988a, b; Duncan and Bird 1989), which might also reflect male hunting ability.

Based on these assumptions, we tested experimentally whether female kestrels prefer relatively small males as mates. We also examined in the laboratory whether female choice could be related to good hunting success of males without the female's prior knowledge of their hunting success. In the field, we also examined the intensity of courtship feeding by different-sized males to find whether small males are good food providers.

Methods

This study was carried out in central Finland, at Konnevesi Research Station (c. 63°N, 23°E). Kestrels (12 males, 14 females) were trapped in western Finland late in the breeding season of 1990, with the permission of the Finnish Ministry of Environment. After the experiment, the kestrels were released in the same area where they were captured. The kestrels were kept in individual cages (2.3 × 1.0 × 1.7 m) in an old farmhouse. In the early spring, about

1 month before the mate choice experiment, the daily light period was abruptly increased from 7 h to 20 h and the females' diet (mainly newly hatched rooster chicks) was increased, to accelerate their sexual activity (see also Meijer 1989).

Female choice experiments

The experimental setup was the same as used in previous studies (see also Duncan and Bird 1989; Hakkarainen et al. 1993; Palokangas et al. 1994). The experimental room (2 × 2 × 1.3 m) consisted of two equal-sized chambers with similar artificial lights (60 W) in both chambers. On the back wall of each chamber we put a nest-box (35 × 35 × 35 cm) suitable for kestrels. During the experiment, one male was accommodated in each of these two chambers and a partition prevented the males from seeing one another. The number of mating options in this experiment was similar to that observed in the field in western Finland; during the 3-year vole cycle, the mean number of unmated males per female was 2.4 (range 1–7; recalculated from Palokangas et al. 1992). A female was placed in a box (35 × 35 × 35 cm) between the two chambers so that she could observe the males at a distance of 2 m through a one-way window, but the males were unable to see her.

Experimental dyads (hereafter referred to as "competing males") were formed from all possible male-male combinations within age classes (e.g. male 1 vs male 2; male 1 vs. male 3, and so on). Thus there were ten experimental dyads of adult males and 21 of young males. Each female was used twice in the experiment with the exception that in five cases the same female was used three times. Females saw each male only once during the experiment. We observed female preference from outside the experimental room through a small one-way window (5 × 10 cm). Female behaviour was observed for 15 min, counting which male she was interested in each minute. Thus we defined a female preference index from each experiment as the sum of the counts for (−) and against (+) the smaller male; −15 meaning that all counts indicated a preference for the smaller male and +15 that all counts indicated a preference for the larger male. Females showed their interest in a male by scanning and trying to get in contact with the preferred male. Although the females were not allowed to copulate with males, this method gives a reliable indication of female mating preference (Palokangas et al. 1994). The partition in the chambers was set to the middle of the one-way window. Therefore, a female could see the males equally well and it was easy to see which male the female was scanning.

Male hunting success

Male hunting success was tested in a laboratory to rule out the possible effects of habitat characteristics (vegetation cover, prey abundance and vulnerability) on hunting success. Hunting success was tested in a cage (5 × 4 × 2.5 m), into which we introduced ten voles (5 *Microtus agrestis* and 5 *M. epiroticus*) in four equal-sized enclosures (2 × 2 × 0.8 m). The enclosures were placed symmetrically around the perch of a sitting kestrel. Because of vole scarcity, some of the voles had to be used in two or three replicates.

The hunting behaviour of each kestrel was recorded during 60 min of continuous observation (Martin and Bateson 1986). Hunting success was estimated as the proportion of hunting attempts that were successful. All males were subjected to the same number of hunting trials. Nishimura and Abe (1988) found that capture success in Ural owls (*Strix uralensis*) increased during poor food conditions. Therefore, male kestrels were fed less than the usual amount for 2 weeks before the experiments, to increase their hunting effort and to reduce variation in body mass.

Body mass, wing and tarsus length were used to estimate falcon size. Body mass of males in our study (mean ± SE = 206 g ± 2, $n = 12$) was similar to that of males observed during courtship in the Scottish grassland areas (208 g ± 3, $n = 17$), whereas in English

farmland males were somewhat lighter during courtship (197 g ± 2, $n = 55$; Village 1990). Thus the body condition and hunting motivation of males in our experiment was similar to that in natural conditions. In addition, body mass of males was strongly positively related to wing length (Spearman correlation, $r_s = 0.58$, $n = 12$, $P < 0.10$), which is a more stable morphological character over time. We also measured hunting success of ten females using the same method.

In addition to evaluating male hunting success in the laboratory, we recorded time budgets of free-living males to estimate the intensity of male courtship feeding in the field. Time budgets were observed at the same site where males were trapped for the laboratory experiment. This study area consisted of flat cultivated fields, with small islands of trees, bushes and rivers. In that area, kestrels bred in nestboxes ($n = 330$) fastened to barns and trees (see Korpimäki and Norrdahl 1991). The time budget observations were carried out in three consecutive years (1991, 1992 and 1993) in which the number of observed pairs was 17, 14 and 10, respectively. Based on snap-trapping of voles, these years could be classified as increasing (1991), peak (1992), and low (1993) vole years (Hakkarainen 1994; K. Norrdahl unpublished work). The intensity of courtship feeding was estimated by counting the number of prey items delivered to females by males before egg-laying. Time budgets were based on observations of 8 h per male on fair weather days. We observed focal pairs with binoculars and telescopes at a distance of 200–500 m from their nests so that their behaviour was undisturbed. Male behaviour was recorded continuously (Martin and Bateson 1986). The observed males were caught at nests using swing-door traps (Korpimäki 1988). Male wing length was measured to the nearest 1.0 mm and body mass to the nearest 1.0 g, to see if male morphological characters were related to the rate of courtship feeding.

Results

Female choice

In trials, female preference was estimated as the difference in size measures of the chosen male relative to the other male. The female preference index was positive if females preferred the larger character and negative if they chose the smaller character. The data from the 31 choice experiments revealed that female preference indices on body mass, wing length and tarsus length of males did not differ significantly from zero as tested by one-sample t-test (means ± SD for body mass 0.16 +7.31, $t = -0.27$, $P = 0.79$; for wing length 1.13 ± 6.70, $t = 0.55$, $P = 0.59$ and for tarsus length $-1.18 ± 7.38$, $t = -1.19$, $P = 0.25$) suggesting that female mate choice was not related to these traits. However, if the body mass difference between the two competing males was more than 12 g (i.e. more than the mean difference in body mass of competing males), female preference indices were significantly lower than when size difference (< 12 g) between competing males was small (t-test, $t = 2.02$, $df = 29$, $P = 0.05$; Fig. 1a), suggesting that large size difference between competing males may bias mate choice toward light males.

Similarly, if the difference in tarsus length between competing males was < 2 mm (i.e. less than the mean difference between competing males), females preferred males equally, whereas if difference was
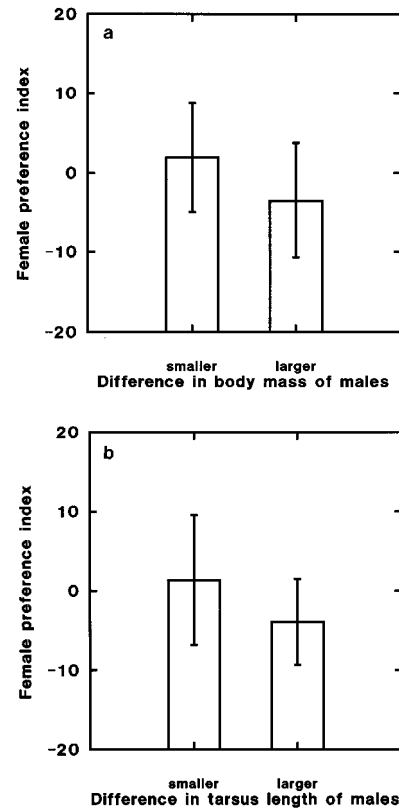

Fig. 1a Preference (−) or avoidance (+) for the lighter male as measured by female prefence index (± SD) in relation to smaller (< 12 g, $n = 21$) and larger ($\geqslant 12$ g, $n = 10$) differences in body mass of competing males. **b** Preference (−) or avoidance (+) for shorter tarsus length of males as measured by female preference index (± SD) in relation to smaller (< 2 mm, $n = 14$) and larger ($\geqslant 2$ mm, $n = 13$) differences in tarsus length of competing males

$\geqslant 2$ mm, then females preferred the males with shorter tarsi (Mann-Whitney U-test, $U = 136.0$, $n = 27$, $P = 0.03$; Fig 1b).

In contrast, females did not prefer males on the basis of wing length. The preference indices between competing males with either small or large differences in wing length (i.e. greater or less than 10 mm difference in wing length) were not significantly different (means ± SD; $1.46 ± 7.46$, $n = 17$ and $0.88 ± 6.47$, $n = 13$, respectively; t-test, $t = 0.23$, $P = 0.82$). This indicates that males were preferred equally despite of the wing length-difference between competing males.

In summary, females seemed to prefer lighter males with shorter tarsi as mates, when the difference in those characters between competing males was relatively large.

Male hunting success

In the hunting experiment, lighter ($r_s = -0.61$, $n = 12$, $P < 0.05$, Fig. 2a) and shorter-winged males
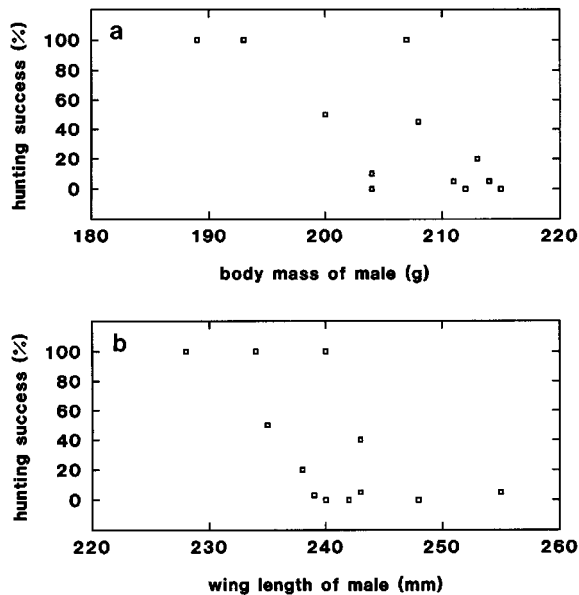
Fig. 2 a Body mass and b wing length of male kestrels in relation to hunting success in an aviary

Fig. 3 Wing length of male kestrels in relation to the number of prey items delivered to the female per hour during courtship

Discussion

Female kestrels preferred to pair with lighter males if the body mass difference between the two competing males was relatively large. Lighter males also exhibited the highest hunting success, suggesting that females may use relative body mass as a cue in mate choice. These findings, together with the observation that shorter-winged males were efficient courtship feeders during a low vole year, when only the best males are able to breed, suggests that males may profit from smaller body size. Therefore, RSD might at least partly result from better mating and hunting success of small males (see also Shine 1988), if the male morphological characters show high heritability (Falconer 1981; Endler 1986). We were unable to determine this, but generally morphological traits are highly heritable (Boag and van Noordwijk 1987), although body mass is often quite variable within individuals (e.g. Bowman 1987). To minimize this within individual variability, males were starved before the hunting experiment (see Witter 1993).

Although hunting and mating success may be independent and separately select for increased RSD, it is probably reasonable to assume that females gain some direct fitness benefits (see also Kirkpatrick 1987; Hoelzer 1989; Palokangas et al. 1994; Wiehn 1997) by choosing a lighter male. Food abundance is the most important determinant of fitness in raptors, suggesting that male provisioning efficiency is one of the most important mate selection criteria for females (see also Simmons 1988a, b; Korpimäki 1989). Female kestrels, however, do not appear to choose males on the basis of their courtship feeding ability (Palokangas et al. 1992). Accordingly, lightness of males may advertise their parental qualities, and female kestrels may be able to advance pair formation and the timing of breeding by using relative male size as a character related to hunting success of males. Preference for shorter-winged males would also profit females, especially because such males were good food provisioners during courtship in poor vole years, when selection on hunting efficiency of males is high. However, in our laboratory experi-

($r_s = -0.52$, $P < 0.10$, Fig. 2b) had better hunting success [(number of prey caught/number of hunting attempts) $\times$ 100] than heavier and longer-winged males. Tarsus ($r_s = 0.05$, $n = 12$, $P > 0.10$) length did not correlate with hunting success. Lighter females were also significantly more successful hunters than heavier females ($r_s = -0.70$, $n = 10$, $P < 0.05$).

A body condition index (body mass/wing length) of males did not correlate significantly with hunting success ($r_s = -0.06$, $n = 12$, $P > 0.10$) or the number of hunting attempts ($r_s = 0.10$, $n = 12$, $P > 0.10$). This indicates that differences in hunting success of males were not due to differences in their fat reserves. Age-related differences could also explain the good hunting success of light males. However, this appeared not to be the case, since the hunting success of yearling and adult males did not differ significantly ($U = 20.0$, $n = 12$, $P = 0.81$). Male body mass was almost the same among yearling (mean $\pm$ SE = 209 $\pm$ 12 g, $n = 7$) and adult males (207 $\pm$ 9 g, $n = 5$; $U = 22.0$, $P = 0.94$).

Examination of courtship feeding in the field revealed that during the low vole year (1993), shorter-winged males provisioned females more than longer-winged males ($r_s = -0.68$, $n = 10$, $P < 0.05$, Fig. 3), although such a relationship was not found with respect to body mass ($r_s = -0.24$, $n = 10$, $P = 0.50$). Neither in the increasing vole year (1991), nor in the peak vole year (1992) was the frequency of courtship feeding significantly related to male wing length ($r_s = -0.05$, $n = 17$, $P > 0.10$ in 1991, and $r_s = 0.52$, $n = 14$, $P = 0.06$ in 1992) or to male body mass ($r_s = 0.29$, $n = 17$, $P = 0.25$ in 1991, and $r_s = 0.33$, $n = 14$, $P = 0.25$ in 1992, respectively).
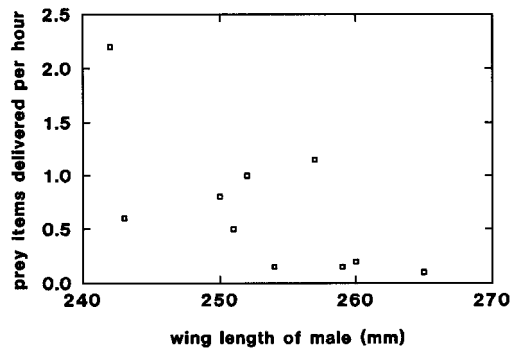
ment, females did not choose their partners on the basis of wing length. This may be because the wing length of competing males may not have been so easy to determine in our experiment, because females did not see the males in flight.

Our results suggest that by choosing lighter males, and probably by choosing shorter-winged males, females may reduce time costs in estimating male quality. For example, evaluating the courtship feeding reliably may take too much time, although courtship feeding influences breeding success (Poole 1985; Daan et al. 1989; Meijer et al. 1989). Quick decision in mate choice is important because the clutch size and reproductive success of most nidicolous birds decreases with later laying date (Klomp 1970; for kestrels see Village 1990; Palokangas et al. 1992; Wiehn 1997).

Some consensus seems to exist that smallness increases the hunting efficiency and success of birds of prey (e.g. Earhart and Johnson 1970; Balgooyen 1972; Reynolds 1972; Andersson and Norberg 1981). In accordance with this, in a low vole year, Tengmalm's owl (*Aegolius funereus*) males with a low body mass in relation to flying area fed their broods more, and produced more fledglings, than did heavier males (Hakkarainen and Korpimäki 1991, 1995). Relatively low body mass obviously decreases the energy costs of flying (see also Balgooyen 1972; Reynolds 1972; Andersson and Norberg 1981), which may be important when hunting areas are large due to food scarcity. In birds of prey, the higher energy expenditure of the male during breeding compared to that of the female (e.g. Masman et al. 1989) may also explain why males have lower wing-loading than females (e.g. Marti 1990 for the barn owl, *Tyto alba*). Female body mass, however, may also influence hunting success as, in the hunting trials, heavier females seemed to have lower hunting success than lighter females. This may balance RSD of raptors by decreasing the benefits attained from large body size of females (e.g. Andersson and Norberg 1981).

In accordance with the energetic hypothesis on RSD, which says that small male size is due to high energy expenditure of males, small male size of some microtine rodents has been found to improve the mobility and mate searching efficiency of males (Bondrup-Nielsen and Ims 1990). Furthermore, in some Diptera species, small and efficient males obtained more copulations than larger males (McLachlan and Allen 1987). In varying food conditions, however, there may be different correlations between male size and feeding efficiency depending upon food abundance. For example, in a peak vole year larger Tengmalm's owl males fed their offspring more than did small males, in contrast to the reverse in a low vole year (Hakkarainen and Korpimäki 1995). Similarly, in a peak vole year, longer-winged male kestrels seemed to be good food providers during courtship feeding, suggesting that in the kestrel phenotypic correlations may also vary in the course of the vole cycle.

If intersexual food competition is considerable, a larger size difference within pairs may reduce food competition between the sexes (e.g. Peters and Grubb 1983; Temeles 1986). In this case, female preference for small male size could reduce overlap in food exploitation by the pair. There are, however, data on food competition between sexes, but three studies have suggested no relationship between degree of dimorphism and reproductive success (Willoughby and Cade 1964; Price 1984; Hakkarainen and Korpimäki 1991).

Female choice should be based on characteristics, which are directly connected with breeding success and which are easy to evaluate in a short time. In the case of the kestrel, these characteristics could be male body size (this study) and coloration (Palokangas et al. 1994). Traditional explanations for RSD so far have focused on explaining why females are larger, mostly emphasizing the high reproductive effort of large females (e.g. Ralls 1976). The present study emphasizes the role of sexual selection in RSD, although we are uncertain about the heritability of the characters studied. More experiments are needed in this context, as the mechanisms explaining SSD seem to be difficult to separate in nature (Hedrick and Temeles 1989).

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