An investigation of mate choice based on manipulation of multiple ornaments in Kentish plovers

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Many animals have multiple sexual ornaments, a fact variously explained as signalling of multiple attributes, or nonadaptive retention of now redundant, but previously informative, signals. Despite the widespread occurrence of multiple ornaments, and the theoretical interest in how they are maintained by selection, there have been few experimental studies of the phenomenon. We investigated the role of two ornaments, each plausibly signalling different male attributes, in attracting a new mate in the Kentish plover, *Charadrius alexandrinus*. Previously we have shown that male Kentish plovers vary in how long they take to acquire a new mate, and we hypothesized that this variation may relate to their attractiveness or parental ability. We created single males by removing their mate and clutch, and then manipulated both their badge size (a presumed signal of either their genetic quality or their dominance status and hence defensive abilities) and the length of their flank feathers (a presumed signal of their parental quality in incubation) in a 2×2 factorial design. We found no difference in remating times between manipulated and control males. Furthermore, neither body size nor body condition of males was related to their remating times, although males with enlarged badges spent less time fighting than control males. Taken together, our results suggest that female Kentish plovers do not use either badge size or the length of flank feathers as cues in their mate choice decisions. However, badge size may influence male–male competition.

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Females use various cues to assess the quality of males, including behavioural displays, advertisement calls, pheromones and morphological traits (Andersson 1994). Females may benefit from mating with high-quality males, because such males may provide direct benefits such as a good breeding territory or increased viability of the offspring through paternal care (Hoelzer 1989; Kokko 1998; Iwasa & Pomiankowski 1999). Alternatively, females may benefit indirectly through favourable genes for increased viability ('good genes') or attractiveness of their offspring (Andersson 1994). Both 'direct' and 'indirect' benefits to female choice have been found in various organisms (reviewed by Andersson 1994; Møller 1994; Qvarnström & Price 2001). In birds, some of the most

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obvious cues used in mate choice decisions are plumage ornaments such as elongated feathers and brightly coloured patches (e.g. Norris 1990; Hill 1991; Møller 1994).

Females often have multiple cues available to them (Brooks & Caithness 1995; Omland 1996), although studies typically investigate the influence of a single trait on female preferences. There are many possible explanations for the evolution and maintenance of multiple ornaments (Møller & Pomiankowski 1993; Johnstone 1995; Brooks 2002). They may reflect the 'ghosts of selection past' such that some traits previously indicated quality or attractiveness or were effective in sensory exploitation, but are now redundant (Holland & Rice 1998). Another explanation for multicomponent male displays may be that different traits may convey information for multiple receivers, for instance one trait may be a signal for females, whereas another may be a signal for other males (Andersson et al. 2002). Multiple signals may also convey information about different aspects of male quality, information that is of different value to different females, or information of different value under different conditions (Candolin 2003). For instance, some

traits may provide information on genetic quality of males ('good genes'), whereas others may signal their parental abilities ('good parent'). Female preferences of multiple traits can be investigated by simultaneously manipulating several ornaments (Ryan 1997), but few studies have attempted this approach.

We manipulated two plumage traits in a precocial shorebird, the Kentish plover, *Charadrius alexandrinus*, a species highly suitable for such a study. First, Kentish plovers have a variable parental care and mating system, since after the eggs hatch, either the male or the female may desert the brood and remate (Székely & Lessells 1993; Fraga & Amat 1996). Female Kentish plovers have better opportunities to acquire a new mate than males do, and the remating time of males is highly variable (range 2.5–48.5 days; Székely et al. 1999). This large variation may be caused by differences in the males' attractiveness, or in their abilities to defend their breeding territories against other males.

Second, Kentish plovers are sexually dimorphic. Males have significantly longer tarsi than females, distinctive black head-bars and one black band on each side of their breast, whereas the females are drab (Székely et al. 1999). During sexual displays males expose their breast bands to females. Black breast bands are secondary sexual traits, and in some passerines females prefer males with large breast bands so this trait appears to be a reliable indicator of genetic quality (Møller 1988; Norris 1993; but see Griffith et al. 1999). In addition, male Kentish plovers have longer flank feathers than females (Kis & Székely 2003). Heat insulation depends on plumage quality (Wolf & Walsberg 2000) and long flank feathers appear to facilitate incubation and brood care; thus long flank feathers may signal the parental ability of males. Efficient incubation and brood care appear to be particularly important in ground-nesting birds such as Kentish plovers, because their eggs and precocial young are exposed to ambient temperatures, and are less protected than the offspring of cavity breeders. Parents may spend over 80% of their time brooding their young while they attend the brood, and parents brood their chicks for over 20 days after hatching (T. Székely, personal observation). Since female plovers often leave brood care entirely to their mate, we predicted they would assess precisely the parental abilities of their prospective mates.

We carried out an experiment in which we manipulated both the size of breast bands and the length of flank feathers in males. Specifically, we tested the hypotheses that breast bands and flank feathers are used by females in mate choice decisions. First, we predicted that if breast bands indicate male quality, then males with enlarged breast bands would find a mate sooner than males with control breast bands. Second, we predicted that if long flank feathers indicate parental ability, then males with shortened flank feathers would need more time to find a new mate than control males.

METHODS

Study Area

We carried out the fieldwork between 6 April and 1 July 1999 in an area of about 140 ha at Tuzla Lake (36°42′N, 35°05′E) in Çukurova-Delta, southern Turkey. Approximately 1000 pairs of Kentish plovers breed in the salt marsh around the lake (see also Székely et al. 1999).

Experimental Protocol

Both parents were caught on their nest by a funnel trap ($N = 60$ pairs). They were ringed with a numbered metal ring and an individual combination of colour rings. We used blue, dark green, light green, orange, red, yellow and white colour rings. Each male had two rings on both his legs (either two colour rings, or one metal ring and one colour ring). We found no indication that colour rings influenced their mating time (analyses not presented). We weighed all plovers with a Pesola spring balance (± 0.1 g), and measured their tarsus with a dial calliper (± 0.1 mm) and their wing length with a ruler (± 1 mm). We also scored their intrafurcular fat reserve by visually estimating the amount of fat on their breast following Helms & Drury (1960). Their eggs were measured and then relocated to other nests that were not included in the experiment. Only pairs with three eggs (modal clutch size) were included in the study.

The male was measured and manipulated (if needed), whereas the female was taken into captivity (see below). We manipulated the size of males' breast bands ('badge' henceforth) and the length of their flank feathers ('flank feathers' henceforth) in a factorial design. Each factor had two levels: badge-enlarged (E) and badge-control (C); flank-shortened (s) and flank-control (c); thus we had Es, Ec, Cs, Cc males, with $N = 15$ in each group. A randomized-block design was used to control for the potential seasonal variation in male quality. Manipulations were carried out between 18 April and 7 June, and within each block males were randomly allocated to the treatments.

After the manipulation the males were released, and we searched for them at least every other day until 30 June. When a male was found we checked whether he had remated. He was considered remated if a female accepted his courtship, with the pair copulating or preparing a nest scrape together or the female permanently following the male (Székely et al. 1999). At least 11 males changed their mate before the first female produced a clutch. One male changed his mate twice, and laid a clutch with the third female. We were able to detect these mate changes because one, both, or in one case, two out of three females were individually ringed.

We recorded the behaviour of males every 20 s over a 30-min period. For each male we aimed to collect behavioural samples three times before they remated and three times after they remated. Several behavioural categories were recorded; here we focus on those related to display behaviour (i.e. courting, nest scraping and fighting with conspecifics). Behavioural observations were carried out by Á.Z.L. and J.K., who used the same behavioural categories and the same methodology. We searched for new nests of remated males and captured, measured and ringed their new females. We also measured the eggs in their new nests.

As in our previous experiment (Székely et al. 1999), removed females were kept in an outdoor aviary near the field site. The aviary consisted of five purpose-built pens (2.5×2.5 m and 0.8 m high). A maximum of five plovers were housed in a pen at the same time. Food and water were available ad libitum and we replenished the supplies twice daily. The food consisted of Haith's Prosecto (a mix for insectivorous birds), live mealworms, boiled rice, chopped pieces of hard-boiled hen eggs and eggshells. In addition, two to four multivitamin droplets were added to their water every day. The Turkish Ministry for Natural Parks licensed the experiment in a location where Kentish plovers are locally very abundant (Magnin & Yarar 1997). After their former mate had remated, the females were released from captivity in the same location where they had been captured. Released females were in good condition; several of them remated with nonexperimental males, laid a new clutch and hatched the clutch successfully.

Measurements and Manipulation of Badges and Flank Feathers

We defined badge size as the sum of the areas of the left and right black patches from the shoulder to the breast of males. We put an overhead-transparency strip tightly around their neck and breast, ensured that the feathers lay flat in their natural position and traced the size of their badge on the strip with a marker pen. We scanned the transparencies and measured the area of badges (mm^2) with Scion Image software (Scion Corporation 1998). Each male's badge was traced twice on one transparency strip each before the manipulation in the field, and in the analyses we used the means of these two measurements (premanipulation badge size).

Badge size was manipulated with Nyanzol D dye flakes (Belmar Inc., North Andover, Massachusetts, U.S.A.). We dyed an area of approximately 25×5 mm in all males. In badge-enlarged males we dyed an area of feathers beneath the original badge area, whereas in badge-control males we dyed the feathers of the original badge itself. The dye was allowed to dry, and then we traced the badge size twice as described above, using the mean (postmanipulation badge size) in later analyses. The repeatability of the measurements was high both before and after manipulation for both right and left sides of black patches ($R_{min} = 0.782$, $R_{max} = 0.926$; $F_{1,60,min} = 8.171$, $F_{1,60,max} = 26.084$, $P < 0.001$; Lessells & Boag 1987). The dye remained black for over 30 days (Á. Z. Lendvai & J. Kis, personal observation). Neither the natural black badge nor the dye reflected in the ultraviolet, and the dyed patches matched natural black feathers across the avian-visible spectrum (I. C. Cuthill & T. Székely, unpublished data; methods as in Cuthill et al. 1999). The size of the manipulated badges overlapped with the natural range of this trait (see also Discussion).

The length of the flank feathers was measured to the nearest millimetre at five points around the sternum: left side, left middle, centre, right middle and right side, referred to as positions −2, −1, 0, +1 and +2, respectively (Kis & Székely 2003). In the analyses we used the mean of these five measurements (premanipulation flank feathers). We measured the length of flank feathers in all experimental males, apart from the first two males, which we missed.

The side feathers (positions +2, −2) are approximately twice as long as the centre and middle feathers (Kis & Székely 2003), so we adjusted the manipulation accordingly. In flank-shortened males we cut approximately 25 mm off the feathers in positions −2 and +2, and approximately 10 mm off the feathers in positions −1, 0 and +1. Flank-control males were not manipulated. An alternative procedure, cutting and regluing the flank feathers, was not practical; since the quills of flank feathers are very thin, regluing these feathers would have taken an unreasonably long time. After manipulation, the flank feathers were remeasured in the same five positions, and we used the mean as postmanipulation flank feathers in the analyses. The repeatability of flank feather measurements was also high in each position ($R_{min} = 0.706$, $R_{max} = 0.931$; $F_{1,28,min} = 5.791$, $F_{1,28,max} = 27.825$, $P < 0.001$, using only flank-control males). After manipulation flank feather length overlapped with the range of natural variation in this trait.

Data Processing and Statistical Procedures

Date of remating was defined as the midpoint between the last date when a male was single and the first date when he was seen with a new mate. Resighting intervals did not differ between the four experimental groups (Kruskal−Wallis test: $H_3 = 3.843$, $P = 0.279$). Remating time was the number of days elapsed from the manipulation date to the date of remating.

Several males had not remated by the time our observations were terminated. We dealt with this in two ways. First, we used binary logistic regression to analyse the effect of treatment and date on the probability of acquiring a new mate (unpaired = 0, paired = 1). Second, to assess effects on the time needed to remate, we used Cox regression for survival analysis (SPSS Inc. 1999), and we refer to these estimates as expected remating times (see also Székely et al. 1999). In the latter analyses the terminal event was remating, and cases where the terminal event had not occurred by the last observation of the focal male, or by the end of the study, were treated as censored (SPSS Inc. 1999). We also investigated the effects of body size (measured as tarsus length), body mass, condition (measured as the amount of fat reserves) and male behaviour (courtship, nest scraping and fighting) on expected remating time using Cox regression. We give the Wald statistic and slope, β, in all cases. Note that for our survival analyses, when β is negative, the independent variable increases the chance of remating; this is because all males start unpaired and the analysis assesses which factors increase the probability of remaining single. For completeness, we also present 'traditional' analysis of variance (ANOVA) results using the log-transformed remating times for birds that found new mates. These do not take account of censored values, but may be more familiar to most readers.

Behavioural variables were calculated as the proportion of observation time when the focal bird was in view. They were square-root transformed and analysed with parametric tests. Each male was included once in the analyses; if several observations were available for a male then we calculated the mean values separately for before and after remating, and randomly selected one of these means.

Hatching success of new nests was low, with only 13% of new clutches hatching at least one chick, and thus hatching success was not compared across groups of males. Instead, we analysed the number of days between laying date and the date of failure or hatching.

Dates are given as number of days since 1 March 1999. Clutch volumes were calculated according to Székely et al. (1994). Two-tailed probabilities and means ± SEs are given unless otherwise indicated. We used SPSS 9.0 for Windows (SPSS Inc. 1999).

RESULTS

Before Manipulation

We found no differences between the four experimental groups in their premanipulation badge size and flank feathers (multivariate analysis of variance (MANOVA): Wilk's $\lambda = 0.929$, $P = 0.682$; badge size: $F_{3,54} = 1.076$, $P = 0.367$; flank feathers: $F_{3,54} = 0.021$, $P = 0.996$). Also, tarsus length, wing length, body mass and date of manipulation did not differ between treatment groups (MANOVA: Wilk's $\lambda = 0.855$, $P = 0.735$; tarsus: $F_{3,56} = 1.118$, $P = 0.350$; wing: $F_{3,56} = 1.330$, $P = 0.274$; body mass: $F_{3,56} = 0.685$, $P = 0.565$; date of manipulation: $F_{3,56} = 0.004$, $P = 0.999$). Finally, there was no difference in intrafurcular fat reserves between the four experimental groups (Kruskal–Wallis test: $H_3 = 3.270$, $P = 0.352$).

Effect of Manipulations

As intended, the manipulation influenced both the badge size and the flank feathers: badge-enlarged males had larger badges than badge-control ones (Es: 403.27 ± 23.85 mm^2; Ec: 391.92 ± 20.74 mm^2; Cs: 249.90 ± 30.40 mm^2; Cc: 269.14 ± 34.83 mm^2; ANOVA for postmanipulation badge size with Bonferroni post hoc tests: manipulations: $F_{3,56} = 7.576$, $P < 0.001$), and flank-shortened males had shorter flank feathers than flank-control ones (Es: 12.87 ± 0.69 mm; Cs: 12.83 ± 0.54 mm; Ec: 28.87 ± 0.50 mm; Cc: 28.74 ± 0.35 mm; ANOVA for postmanipulation flank feather length with Bonferroni post hoc tests: manipulations: $F_{3,54} = 303.843$, $P < 0.001$).

Remating Time

The probability of remating was strongly affected by the breeding season, males having a higher probability of remating early in the season (binary logistic regression: breeding season: $\beta = -0.083$, Wald statistic = 12.946, $P < 0.001$). However, besides the seasonal effect, the manipulations did not influence a male's chances of acquiring a new mate (binary logistic regression: breeding season:

$\beta = -0.089$, Wald statistic = 13.161, $P < 0.001$; badge size: $\beta = 0.060$, Wald statistic = 0.004, $P = 0.945$; flank feathers: $\beta = 0.522$, Wald statistic = 0.299, $P = 0.584$; badge size × flank feathers interaction: $\beta = -1.716$, Wald statistic = 1.654, $P = 0.198$). The nonsignificant pattern was the same as that observed for expected remating times (see below).

For those males that found new mates, remating did not differ between the four experimental groups (ANOVA: badge size: $F_{1,34} = 0.145$, $P = 0.706$; flank feathers: $F_{1,34} = 0.377$, $P = 0.543$; badge size × flank feathers interaction: $F_{1,34} = 0.063$, $P = 0.803$; Fig. 1). When we used survival analysis to account for the censored values, the expected remating times still did not differ between treatments, but increased with the breeding season (Cox regression: badge size: $\beta = 0.177$, Wald statistic = 0.154, $P = 0.693$; flank feathers: $\beta = 0.456$, Wald statistic = 1.052, $P = 0.305$; badge size × flank feathers interaction: $\beta = -0.735$, Wald statistic = 1.220, $P = 0.269$; breeding season: Wald statistic = 7.321, $\beta = -0.031$, $P = 0.007$; Fig. 2). The expected remating time was also unrelated to tarsus length, body mass or the amount of fat reserves of males (Cox regression: tarsus length: $\beta = -0.265$, Wald statistic = 2.508, $P = 0.113$; body mass: $\beta = 0.004$, Wald statistic = 0.004, $P = 0.949$; fat reserves: $\beta = -0.438$, Wald statistic = 2.390, $P = 0.122$). In addition, male behaviour before remating did not influence the expected remating time (Cox regression: courtship: $\beta = -0.264$, Wald statistic = 1.390, $P = 0.238$; nest scraping: $\beta = 0.003$, Wald statistic = 0.011, $P = 0.950$; fighting: $\beta = -0.136$, Wald statistic = 0.341, $P = 0.559$).

After remating, at least 10 males changed mates once, and one male changed his mate twice. These 11 males remated faster than males that were observed to remate only once (two-sample t test: $t_{36} = 2.618$, $P = 0.008$).
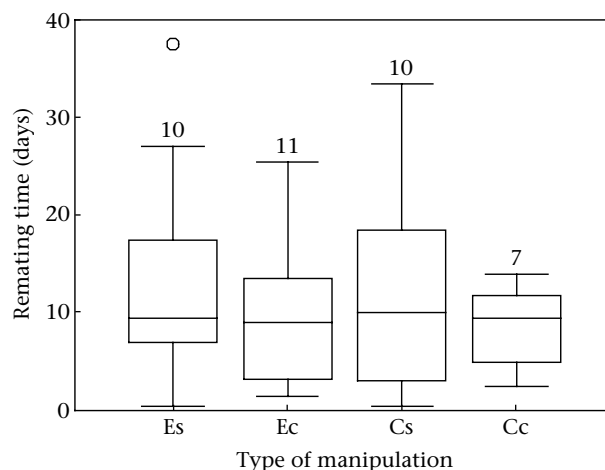

Figure 1. Boxplots of the remating times of male Kentish plovers that acquired new mates. For each box, the central line represents the median, and the bottom and top of the box are the lower (Q1) and upper quartiles (Q3), respectively. The whiskers extend to the lowest and highest observations, respectively, within the range defined by $Q1 - 1.5 \times (Q3 - Q1)$ and $Q3 + 1.5 \times (Q3 - Q1)$. The circle indicates an outlier. Sample sizes are given above the boxes. E/C: enlarged/control breast badge; s/c: shortened/control flank feathers; in 2×2 factorial combination.
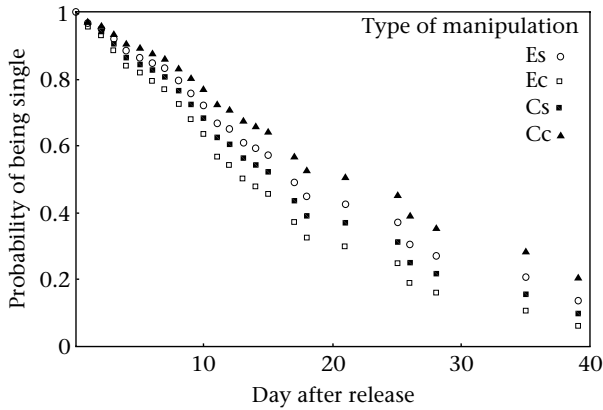
Figure 2. Probability of remaining single after the manipulation in male Kentish plovers. Plovers were released on day 0. E/C: enlarged/control breast badge; s/c: shortened/control flank feathers; in 2×2 factorial combination.
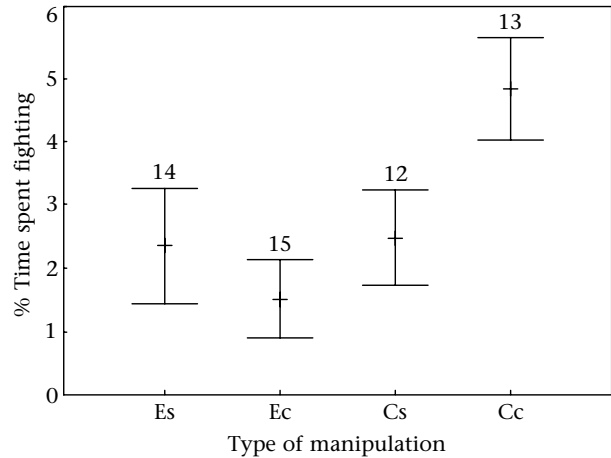

Figure 3. Percentage of time spent fighting (mean $\pm$ SE, $N = 54$ males). Sample sizes are given above the lines. E/C: enlarged/control breast badge; s/c: shortened/control flank feathers; in 2×2 factorial combination.

Behaviour of Males

The transition from being unpaired to paired influenced the behaviour of males, since males with a new mate spent more time nest scraping and courting than single males, although the time spent fighting did not differ before and after remating (Table 1). Manipulations of badge size, but not of flank feathers, influenced the behaviour of males (MANOVA: mating status: Wilk's $\lambda = 0.731$, $P = 0.002$; badge size: Wilk's $\lambda = 0.825$, $P = 0.034$; flank feathers: Wilk's $\lambda = 0.915$, $P = 0.250$), but the date of manipulation was unrelated to male behaviour (covariate: breeding season: Wilk's $\lambda = 0.974$, $P = 0.782$). The significant effect of badge size on behaviour was due to badge-enlarged males spending less time fighting than control males ($F_{1,48} = 7.418$, $P = 0.009$; Fig. 3). However, there was a marginally nonsignificant interaction between badge size and flank feathers ($F_{1,48} = 4.003$, $P = 0.051$), suggesting that badge manipulation had a greater effect in the control-flank groups. In a univariate analysis of fighting, the main effect of badge size remained significant when we considered only fights between males and excluded fights with females or families (ANOVA: $F_{1,48} = 4.222$, $P = 0.045$).

New Mates and New Nests

We found no difference between experimental groups in clutch survival, laying date or volume of their new clutch (MANOVA: badge size: Wilk's $\lambda = 0.789$, $P = 0.203$; flank feathers: Wilk's $\lambda = 0.940$, $P = 0.752$; Table 2).

DISCUSSION

Remating Time

In this study we found no differences in remating time between the four experimental groups. We propose several explanations for this result. First, we may have failed to detect an actual difference between experimental groups. We chose a sample size ($N = 60$) with a high power (>0.8) to detect a difference in remating time of 7 days, based on the variance in remating times observed previously (Székely et al. 1999). Our expectation was that much of the large variation in remating time (from under 3 days to more than 48 in Székely et al. 1999) would be attributable to differences in male attractiveness. We observed similarly large variation in remating time in the present study (>30 days) but, as the nonsignificant treatment effects show, there is no evidence that this was due to differences in badge or flank feather size. From the effect sizes observed in our experiment, the most we can conclude is that if there is an effect on remating time, it is small (<2 days) and not even consistently in the predicted direction (e.g. in the badge control group flank-control males actually showed a trend towards longer remating times than flank-shortened males).

Second, our manipulations might have produced somehow unnatural traits and the statistically nonsignificant differences between treatment groups may be the result of these 'unnatural' males. This explanation is unlikely because both our enlarged badge sizes (205–669 mm^2) and the length of shortened flank feathers (8–35 mm) overlapped with the natural range of these traits (45–372 mm^2 and 14–46 mm, respectively). In addition, our conclusions do not change qualitatively if we restrict the analyses to those males in which post-manipulation badge size and flank feather length were within the natural range.

Table 1. Behaviour of single and remated plovers, as a mean percentage of total observation time $\pm$ SE

	Single	Remated	$F_{1,49}$	P
Courting	5.0 $\pm$ 0.7	10.0 $\pm$ 2.3	5.694	0.021
Nest scraping	3.4 $\pm$ 1.0	12.6 $\pm$ 2.6	16.852	<0.001
Fighting	2.7 $\pm$ 0.5	2.9 $\pm$ 0.8	0.257	0.615

$N = 54$ males; F values and probabilities are given from the between-subject effects of a MANOVA model.

Table 2. Clutch survival, clutch volume and laying date of clutches of remated males

	Type of manipulation			
	Es	Ec	Cs	Cc
Clutch survival (days)	15.80 ± 3.0	16.44 ± 3.0	13.20 ± 3.8	9.83 ± 2.9
Clutch volume (cm³)	23.44 ± 0.7	22.15 ± 1.2	23.03 ± 1.5	24.29 ± 0.4
Laying date (days after 1 March)	92.00 ± 4.0	96.22 ± 3.5	79.60 ± 7.8	87.50 ± 8.0

$N = 25$ males. Means are given ± SE. E/C: enlarged/control breast badge; s/c: shortened/control flank feathers; in 2×2 factorial combination.

Finally, it is possible that neither badge size nor the length of the flank feathers plays a role in female choice, and thus that females use other cues in mate selection. For instance, Amat et al. (1999) found that female Kentish plovers were mated to males with a wider black forehead bar in the first nesting attempt than in the second. Amat et al. suggested that in the first nesting attempt females may use the forehead bar as a cue of individual male quality, whereas in the second they are less choosy and mate with any available male. Although the forehead bar seems less conspicuous to human eyes than the badge, we cannot rule out that this trait is used in mate choice in plovers. In the collared flycatcher, *Ficedula albicollis*, of several morphological characters measured, only the size of the male's white forehead patch is involved in mate choice and aggressive interactions (e.g. Pärt & Qvarnström 1997).

Alternatively, females may choose a male on the basis of his behaviour. Male plovers show complex courtship displays including scraping nests. Females appear to test the nest scrapes by sitting in them, and then may let the male copulate. Although we found no evidence that the time males spent courting or nest scraping influenced male remating times, the position or size of the nest scrapes rather than badge size may be used as an indicator of male quality. Similarly, females may use more direct and reliable indicators of parental abilities than the length of flank feathers; for example, the number of fledglings in a brood cared for only by the male parent may be an honest signal of parental ability. In line with the latter argument we noted that males attending near-fledged young appeared to be more successful in securing a new mate than males with no accompanying offspring (J. Kis & T. Székely, personal observation).

Let us suppose that our experiment had detected different remating times between treatment groups, as predicted. Would these results provide unambiguous support for good genes and good parent processes? The relations between plumage traits and their hypothesized functions may not be as straightforward as we initially envisaged. For instance, badge sizes may signal any qualities of males including parental abilities, and feather length may indicate other male qualities including viable genes. More sophisticated experiments are essential to tie these male plumage traits to paternal behaviour and offspring viability.

Although in this study we did not find evidence that either badges or flank feathers influence female choice, Kentish plovers do show sexual dimorphism in both traits. First, males have black, melanin-based badges whereas females are drab, and we found that badge-enlarged males

spent significantly less time fighting than badge-control ones. This result suggests that badges may be used as a signal in an agonistic rather than a courtship context. Similar conclusions have been drawn in several passerines in which melanin-based coloration did not function in mate choice, but instead played a role in male–male competition (reviewed by Senar 1999).

Second, male Kentish plovers have longer flank feathers than females (Kis & Székely 2003). Although in the current study the manipulation of flank feathers did not influence remating times, the sexual difference in flank feather length may be caused by the greater involvement of the male in parental care. Males are more likely than females to tend their chicks alone and also provide care for longer. Enlarged flank feathers may thus be a (naturally selected) male adaptation for parental care and not a sexually selected ornament. We recommend further studies to investigate the role of badges and flank feathers in intrasexual interactions.

We found that the expected remating time increased over the breeding season, and many males remained unpaired at the end of the field study. The latter result is consistent with a previous experiment in the same population (Székely et al. 1999), and is probably due to the seasonal decline of ecological conditions, such as food abundance, and also to the decrease in the number of available females.

Mate Switching

The remating times of mate-switching males were shorter than those of nonswitching males. This could be because males that find a mate easily are less choosy. It seems that these males paired up with the first available female, but changed mate when they had a chance to pair with a higher-quality female. Alternatively, mate switching may be driven by females, that is, they may reject the male after spending a period of time with him. Finally, paired females may be ousted by another female, for instance if the male is of high quality.

We lack the necessary data to distinguish between these explanations, but note that paired birds may sometimes desert their mates in favour of another partner (Otter & Ratcliffe 1996; Olsson et al. 2001). Our results are consistent with the suggestion that pair formation involves several stages of decision (Candolin & Reynolds 2001). For instance, birds that have initially accepted a partner on the basis of an ornamental cue, or some other visually detectable physical feature, may change partner if

their mate delays egg laying or performs worse (e.g. in displays) than other potential partners (Choudhury 1995).

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