SEXUALLY DIMORPHIC BREAST-FEATHERS IN THE KENTISH PLOVER CHARADRIUS ALEXANDRINUS

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Secondary sexual traits (such as badges and other ornaments) may signal the attractivity of a male for females, or they may reflect its parental quality. We studied the natural variation in breast-feathers in a small wader, the Kentish Plover. We hypothesised that males may have longer breast-feathers than females, because males display these feathers during courtship and male-male contests. Also, males may need longer breast-feathers to provide an efficient incubation. We measured the length of breast-feathers in both sexes and found that lateral feathers were significantly longer than the central ones in both males and females. We also found that breast-feathers tended to be longer in males, especially the central ones, than in females. The mean length of breast-feathers decreased over the breeding season in males, although this relationship was not significant in females. Taken together, our results suggest a moderate difference in breast-feathers between the sexes. We suggest that this difference is due to sexual selection and/or natural selection to achieve more efficient incubation of the eggs.

Keywords: sexual selection, mate choice, parental care, Kentish Plover, *Charadrius alexandrinus*

INTRODUCTION

Breast-feathers of birds are adapted to various roles. First, in many birds, like cranes, waders and passerines, males display their breast-feathers to females during courtship (PERRINS 1998), and thus breast-feathers appear to have a role in mate choice and sexual selection (reviewed by ANDERSSON 1994, SAVALLI 1995). For instance, granivorous passerines such as the Linnet *Carduelis cannabina* and the House Finch *Carpodacus mexicanus* display their colourful breasts to females, and males of waders, such as the Kittlitz's Plover *Charadrius pecuarius* approach females with fluffed breast-feathers (PERRINS 1998, BRAWNER *et al.* 2000). Second, males of some herons, (e.g. the Bittern *Botaurus stellaris*) and waders (e.g. the Piping Plover *Charadrius melodus*) display their breast-feathers in territory defence against intruding neighbours (PERRINS 1998, CAIRNS 1982). Third, breast-feathers are also important in parental care. For instance, sandgrouse have specially adapted feathers to transport water to their chicks (HOYO *et al.* 1996). Furthermore, it is perceivable that efficient incubation and brooding requires feathers

of good insulating capacities since thermal resistance of the plumage depends on the quality of feathers (WOLF & WALSBERG 2000). Therefore, breast-feathers that cover the eggs or chicks are important both in incubation of the eggs and brooding the chicks. Breast-feathers are particularly important in ground-nesting birds that breed on frozen tundra (e.g. sandpipers and *Pluvialis* plovers PIERSMA & MORRISON 1994, HOYO *et al*. 1996), or in hot deserts (e.g. stone-curlews, Inland Dotterel *Peltohyas australis*, HOYO *et al*. 1996). These various functions of breast-feathers may be present in a single species. For instance, males of several *Charadrius* plovers show similar displays in antagonistic contest and during courtship (PERRINS 1998), and these males may also indicate their ability to incubate ('good parent process', HOELZER 1989).

We investigated the natural variation of breast-feathers in the Kentish Plover *Charadrius alexandrinus*. Kentish Plover is a ground-nesting wader that has a sexually dimorphic plumage during the breeding season. Males have an orange-cinnamon crown and black stripes on their forehead and their breast, whereas the females are completely drab. During courtship, males display their breast-feathers to females (GLUTZ VON BLOTZHEIM 1975). Breast-feathers are also displayed during fighting with conspecifics (GLUTZ VON BLOTZHEIM 1975). Both sexes incubate the eggs and brood the chicks, although typically the female parent deserts the brood shortly after the hatching of the young (PATON 1995, AMAT *et al*. 1999, SZÉKELY & CUTHILL 2000). Apart from plumage, there is a slight sexual dimorphism in tarsus length: males are larger than females (SZÉKELY *et al*. 1999).

We studied the length of breast-feathers in the Kentish Plover. We hypothesised that the length of breast-feathers are longer in males than in females, because males incubate the eggs at night when ambient temperatures are lower than during daytime when mostly the females incubate (KOSZTOLÁNYI & SZÉKELY 2002). Also, males display these feathers during courtship and male-male contest, thus these feathers appear to have a role in mate choice by females. We investigated this hypothesis by measuring the length of breast-feathers in both males and females.

METHODS

Field work was carried out between 6 April and 1 July in 1999 at Lake Tuzla, Çukurova Delta, Southern Turkey (36°43'N, 35°03'E). About 1000 pairs of Kentish Plover bred around the lake. We studied the plovers on the north-eastern coast of the lake on an area about 140 ha. The study site was a saltmarsh covered with mudflats alternating with patches of *Salicornia europaea* and *Atrocnemum fruticosum* (SZÉKELY *et al*. 1999, SZÉKELY & CUTHILL 2000).

We caught both the male and the female on their nest (n = 58 pairs). Only pairs with clutches of three eggs (modal clutch size) were included in the study. We estimated the age of the plovers by calculating their minimum age. For instance, if a bird had been caught in 1998 as an adult, its minimum

age was two years, whereas an adult that was caught for the first time in 1999 was considered one year old. Males and females may reproduce at the age of one year. Minimum age was logarithmically transformed (ln) before data processing. Clutch volume (cm^3) was the sum of egg volumes. Egg volume was calculated as $0.486 \times length \times breadth^2$ (SZÉKELY *et al.* 1994). We defined laying date as the number of days elapsed since 1 March until the laying day of the 3rd egg. Laying date was estimated for those nests we found after the clutch was completed (KIS & SZÉKELY unpubl. data).

We measured the length of breast-feathers in five points on the breast of both males and females whilst the bird was hold in hand on its back. The central point, hereafter referred to as "feather (0)", was on the tip of the sternum's keel. Feathers (–2) and (+2) were on the right and left sides of the breast, respectively, where the carpal joints of the closed wings met the body. Feathers (–1) and (+1) were halfway between (–2) and (0) and between (+2) and (0), respectively. The maximum length of feathers in each point was measured with a ruler to 1 mm. The measurements were repeatable based upon 28 males and 54 females that were measured twice (males: $r = 0.706–0.931$ (range), $F_{1,27} = 5.791–27.825$ (range), $P < 0.0005$ in all positions; females: $r = 0.535–0.869$ (range), $F_{1,27} = 3.305–14.235$ (range), $P < 0.0005$ in all positions, LESSELLS & BOAG 1987). If two measurements were available for the same position, we used their means in the analyses. All measurements were carried out by J.K.

To investigate plumage profiles of males and females we used repeated measures ANOVAs in which feather positions (–2, –1, 0, +1, +2) were the within subject factors. For the comparison of sexes, we used double-repeated measures ANOVAs in which feathers and sex were the within-subject factors. We compared the differences between pairs of feathers with pairwise comparisons of the repeated measures ANOVA that furnishes exact significance levels. These significance levels were corrected by the sequential Bonferroni method (RICE 1989).

We used Pearson correlation coefficients (r_p), or Spearman correlation coefficients (r_s) when the assumptions of normality or the homogeneity of variances were violated. We provide the mean ± SE and two-tailed probabilities. We give the observed power (OP) for statistically non significant results. Data analyses were carried out using SPSS 9.0 for PC.

RESULTS

The length of breast-feathers was different between feathers (–2, –1, 0 +1, +2) in both sexes (repeated-measures ANOVA, males: $F_{4,54} = 1156.019$, $P < 0.0005$; females: $F_{4,54} = 1089.088$, $P < 0.0005$; Table 1, Fig. 1). In both sexes, the central feathers (–1, 0, +1) were shorter than the lateral ones (–2, +2) as showed by pairwise comparisons (Table 2). In males, feather (–2) was shorter than feather (+2) (Table 2), whereas the central feathers (–1, 0, +1) were not significantly different from each other (Table 2). In females, neither right and left lateral feathers (–2, +2), nor feathers (–1) and (+1) were significantly different from each other. On the other hand, in females feather (0) was shorter than both (–1) and (+1) (Table 2).

Breast-feathers tended to be longer in males than in females ($F_{5,53} = 2.274$, $P = 0.060$, OP = 0.690; double-repeated measures ANOVA, within subject factors: feather position and sex). We also investigated which feathers were the most different between the sexes and we found that feather positions (–1, 0) differed, while

Table 1. Sexual dimorphism in the length of breast-feathers in the Kentish Plover (mean ± SE mm). OP is the observed statistical power of the tests

Position	males	females	$F_{1,57}$	P	OP
−2	39.94 ± 0.33	39.62 ± 0.32	0.446	0.507	0.101
−1	21.28 ± 0.22	20.62 ± 0.19	6.065	0.017	0.678
0	21.17 ± 0.26	19.99 ± 0.27	10.343	0.002	0.885
+1	20.92 ± 0.20	20.53 ± 0.18	2.439	0.124	0.336
+2	40.64 ± 0.35	39.84 ± 0.39	2.802	0.100	0.377

the lengths of the other feathers were not significantly different between the sexes (Table 1).

We also calculated the mean length of breast-feathers separately for males and females by averaging the lengths of feathers (−2, −1, 0, +1, +2). Mean breast-feather length decreased during the breeding season in males but it was unrelated to the breeding season in females (Table 3, Fig. 2). Clutch volume and minimum age were unrelated to mean breast-feather length (Table 3). We further investigated whether the relationship between laying date and mean breast-feather length was specific to some of the breast-feathers. Interestingly, the analyses showed that the central feathers (−1, 0, +1) significantly decreased over the breeding season in both males and females (males: P = 0.001–< 0.0005 (range); females: 0.001–< 0.0005 (range)), although the lengths of lateral feathers (−2, +2) were un-
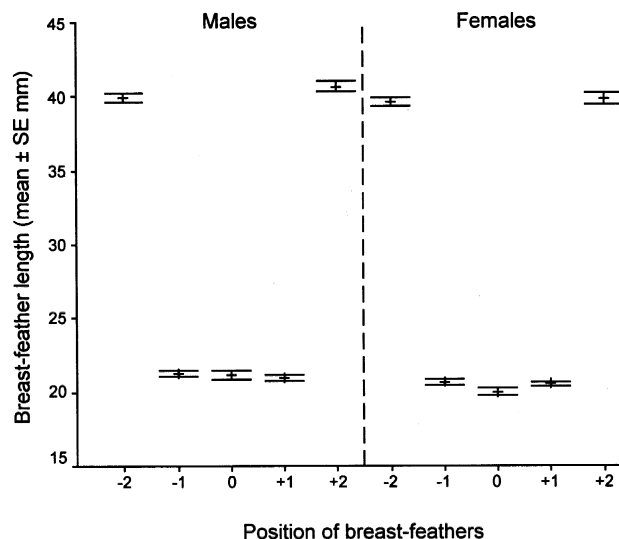

Fig. 1. Plumage profiles of male and female Kentish Plovers

related to the breeding season (males: P = 0.116–0.516 (range); females P = 0.197–0.618 (range)).

Finally, there was no relationship between males and females in the mean length of breast-feathers within a pair (r_p = –0.018, P = 0.891, N = 58 pairs).

Table 2. Pairwise comparisons between feather positions. Repeated measures ANOVA. **N** is the rank of the pair of feather positions of the P-value and α is the critical acceptance level corrected by the sequential Bonferroni method. Pairs with significant differences are in bold. Pairwise differences between lateral (–2, +2) and central (–1, 0, +1) feathers are given below the line

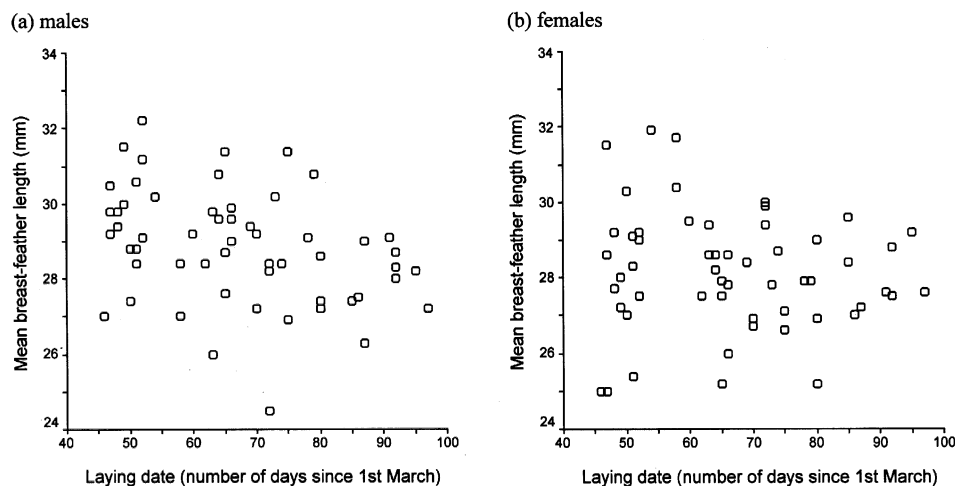| N	α	Males		Females	
		pairs	P	pairs	P
1	0.050	–1, 0	0.620	–1, +1	0.528
2	0.025	0, +1	0.344	–2, +2	0.414
3	0.017	–1, +1	0.081	**0, +1**	0.010
4	0.013	**–2, +2**	0.006	**–1, 0**	0.002
5	0.012	**–2, –1**	< 0.0005	**–2, –1**	< 0.0005
6	0.009	**–2, 0**	< 0.0005	**–2, 0**	< 0.0005
7	0.007	**–2, +1**	< 0.0005	**–2, +1**	< 0.0005
8	0.006	**–1, +2**	< 0.0005	**–1, +2**	< 0.0005
9	0.006	**0, +2**	< 0.0005	**0, +2**	< 0.0005
10	0.005	**+1, +2**	< 0.0005	**+1, +2**	< 0.0005

(a) males

(b) females

Fig. 2. The length of mean breast-feathers in the Kentish Plover in relation to the date of egg-laying. (a) males: r_s = – 0.391, P = 0.003, N = 57; (b) femalesy: r_s = – 0.131, P = 0.332, N = 57

Table 3. Relationship between laying date, clutch volume and minimum age and the mean length of breast-feathers in the Kentish Plover (multiple least-squares regression; mean breast-feather length with laying date, clutch volume and minimum age; males: $F_{3,53} = 3.508$, adjusted $R^2 = 0.118$, $P = 0.021$; females: $F_{3,53} = 1.279$, adjusted $R^2 = 0.015$, $P = 0.291$, OP $= 0.322$. OP is the observed statistical power of the tests

	B	t	P	OP
Males				
Intercept	28.572	13.007	0.000	1.000
Laying date	−0.046	−3.239	0.002	0.889
Clutch volume	0.000	1.382	0.173	0.274
Minimum age	−0.183	-0.465	0.644	0.074
Females				
Intercept	26.510	11.262	0.000	1.000
Laying date	−0.023	−1.502	0.139	0.314
Clutch volume	0.000	1.271	0.209	0.239
Minimum age	−0.581	−1.313	0.195	0.252

DISCUSSION

Male and female Kentish Plovers have a similar pattern in their breast-feather profiles: long lateral feathers (−2, +2) and short central feathers (−1, 0, +1). There are, however, slight gender differences in these profiles. The central feather (0) is approximately at the same length as (+1) and (−1) in males, but it is significantly shorter in females. This difference (6.4 % for feather (0) of the mean for females) may simply be the result of allometry, since males have slightly longer tarsi than females (SZÉKELY *et al.* 1999). However, this is unlikely because these trends remained in the same direction when we controlled for body size. ROWE *et al.* (2001) showed that both natural and sexual selection might have contributed to sexual differences in the length of the tail streamer in the barn swallow *Hirundo rustica*. The slight gender difference in plumage profiles of Kentish Plovers may be particularly important in this species, which has a variety in mating and parental care systems. In sex-role reversed species (e.g. jaçanas and phalaropes; EMLEN *et al.* 1998, REYNOLDS 1987), females are brighter and bigger than males, court males, hold territories and do not care for the young. In contrast, male Kentish Plovers are brighter than females, they court females, hold territories, although they are more likely to care for the offspring alone than females. Breast-feathers seem to be important in incubation and the brooding of chicks. In Kentish Plovers, both sexes take part in both incubation and brood-rearing (KOSZTOLÁNYI & SZÉKELY 2002,

SZÉKELY & CUTHILL 2000). Thus, perhaps in the Kentish Plover selection may act on both males and females to develop long breast-feathers.

Long central feathers may have a further advantage for males. Males incubate mostly during the night (KOSZTOLÁNYI & SZÉKELY 2002). Therefore males with longer feathers may lose less energy and/or may allocate more energy to the eggs than males with short feathers. On the other hand, natural selection on females that mostly incubate during day-time, may be less intense. Further experiments of mate choice, male-male competition and parental abilities in incubation and brooding in relation to breast-feathers are warranted to identify and separate these selective forces.

Clutch volume and age did not relate to the length of breast-feathers in either sex. Early breeding males had longer feathers than later breeders. This relationship was not significant in females. Interestingly, only the central feathers (-1, 0, $+1$) changed with laying date in males. Although we did not find a significant relationship in females, the same trend was apparent. Plovers with long feathers may be able to start to breed earlier than short-feathered individuals. The timing of breeding is important in both sexes, because chicks hatched later in the season had lower survival than chicks hatched earlier, and in addition, birds that breed earlier are more likely to have a second brood (SZÉKELY & CUTHILL 1999). Therefore, individuals with long feathers probably have an advantage via earlier and/or more breeding opportunities.

In conclusion, our studies showed sex differences in breast-feathers in the Kentish Plover. We suggest that these differences are related to the strength of sexual selection and/or natural selection. We recommend further experiments to separate the influences of these selective processes on the evolution of plumage traits in the Kentish Plover.

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