

Male badge size is related to clutch volume in the Kentish Plover

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Shorebirds show large interspecific variability in melanin-based breast coloration, although the adaptive value of this trait is largely unknown. In this study, we investigated whether variation in the size of breast bands (badge) in male Kentish Plovers (*Charadrius alexandrinus*) is related to the start of their breeding and volume of their clutches. We found that males with large badges started breeding earlier than males with small badges. Large-badged males also had larger clutch volumes than males with smaller badges, after controlling for seasonal effects. These results suggest that large-badged male Kentish Plovers may have a reproductive advantage over small-badged ones, because usually both early breeding and large egg volumes increases reproductive success in shorebirds. These results suggest that badge size may signal male quality that affects either the females' investment in eggs or the success of males in territory defence.

Key words: sexual selection, cryptic female choice, melanin, egg size, *Charadrius alexandrinus*.

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1. Introduction

Plovers and their allies (suborder Charadrii) exhibit a large interspecific variation in melanin-based black breast coloration (Bókonyi *et al.* 2003). Although the variability of these melanin ornaments have drawn the attention of researchers for a long while (*e.g.* Bock 1958, Graul 1978), their adaptive value is still poorly known. The few studies carried out in plovers and allies have suggested two main functions of these melanin ornaments. First, melanin plumage ornaments may be signals of individual quality that affects mating success via mate choice and/or success in intrasexual contest for mating partners

(Edwards 1982, Owens *et al.* 1994, Bókonyi *et al.* 2003). Second, melanin-based colours may have roles in territory defence, because variable plumage badges may promote neighbour recognition and thus may facilitate territory defence against unfamiliar intruders (Whitfield 1986).

In this study, we investigated the significance of male breast band size for breeding in the Kentish Plover (*Charadrius alexandrinus*), a small ground-nesting shorebird. Kentish Plovers are sexually dichromatic birds: females are drab, whereas males have black eye stripes, a horizontal head bar, and two conspicuous black breast bands ('badge' henceforth), one on each of the right and

left side of their white breast plumage. Amat *et al.* (1999) suggested that females may use the head bar as a cue of male quality during mate choice. Observations suggest that breast plumage may also be important for breeding: during courtship and male-male conflicts, males display their badges by puffing up their breast feathers (Perrins 1998). Furthermore, Lendvai *et al.* (2004) showed that large-badged males may have an advantage in aggressive male-male encounters. Note that sexual selection should be intense in this species because mate desertion and sequential polygamy are frequent in most populations (*e.g.* Székely & Cuthill 1999 and citations therein).

In this study, we used field observations to investigate whether variation in badge size is related to components of sexual selection. According to sexual selection theory, we hypothesized that badge size may be a signal indicating male quality. One prediction of this idea is that males with large and conspicuous badge size are able to acquire better quality mates who produce larger number and/or more viable offspring than mates of small-badged males. As shorebirds are determinate layers (*e.g.* Kentish Plovers usually have a clutch of three eggs), we used clutch volume as a surrogate to estimate female quality.

2. Methods

We carried out the fieldwork between 18 April and 7 June 1999 in an area of about 140 ha at Tuzla Lake (36° 42' N, 35° 05' E) in the Çukurova-Delta, southern Turkey. Approximately 1000 pairs of Kentish Plover breed around the lake each year.

The study site is a salt marsh, where bare patches of mudflats alternate with patches of *Artrocnemum fruticosum*, *Salicornia europea* and other halophytes. The study was licensed by the Turkish Ministry for Natural Parks (licence number: 880973/06/04/1999).

We searched for nests throughout the breeding season, and we measured the size of the eggs for each clutch. Clutch volume (mm³) was calculated as the sum of egg volumes, where egg volume was estimated as $0.486 \times \text{length} \times \text{breadth}^2$ (Székely *et al.* 1994). All studied nests ($n=60$) contained 3 eggs. We defined laying date as the number of days elapsed since 1 March until the laying of the 3rd egg. For nests found after the clutch completion, laying date was estimated by floating eggs in lukewarm water (van Paassen *et al.* 1984, and J. Kis & T. Székely unpubl. data).

We caught both the male and female on their nest by a funnel trap ($n=60$ pairs) 4.3 ± 2.9 (mean \pm SD) days after clutch completion. They were ringed by a numbered metal ring and an individual combination of colour rings. Their body mass (± 0.1 g), tarsus (± 0.1 mm) and wing length (± 1 mm) were measured. In males, we measured the size of their breast bands (badge) as the sum of the left and right black patches, measured from the shoulder to the breast. We put an overhead transparency strip tightly around the birds' neck and breast, and traced the size of their badge on the strip with a marker pen. We scanned these transparencies and measured the area of badges in mm² using Scion Image software (Scion Corporation 1998). Badge area was traced and measured twice for each male and we used the mean of these two measurements in the analyses. The repeatability of badge size

was high ($R=0.941$, $F_{1,60}=17.127$, $P<0.0001$; Lessells & Boag 1987). Finally, we also estimated the minimum age of the plovers, *i.e.* we knew the age of birds ringed as chicks and assumed that birds ringed as breeding adults were one year old in the year of ringing (minimum age ranged from 1 to 4 years).

Each male was included once in each analysis, *i.e.* we used data from the first known nests of the males. We used multivariate linear regression models to investigate the relationships of male badge size to male and female characteristics and clutch volumes. We used Spearman rank correlation to investigate the relationships of male badge size to age, because the latter variable could not be included in parametric models without violating their assumptions. We used SPSS 11.0 for Windows for statistical testing, and give two-tailed probabilities and mean $\pm SE$ throughout the paper.

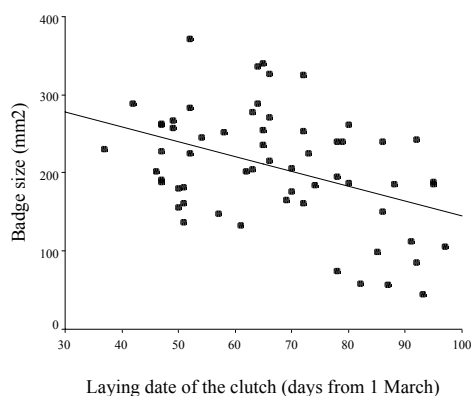


Fig. 1. Relationship between the breeding date of male Kentish Plovers ($n=60$ males) and their badge size.

3. Results

3.1. Body size characteristics and laying date

Male badge size was related to the laying date of clutches: males with early nests had larger badges than males with late nests (Tab. 1., Fig. 1.). Neither body size (measured as tarsus and wing length) nor body mass of males was related to badge size; furthermore, male badge size was not related to the female mate's tarsus length, wing length, and body mass in a model that also controlled for the effects of laying date (Tab. 1.). Variation in badge size was also unrelated to the minimum age of males ($r_s=0.193$, $P=0.139$, $n=60$), and to the minimum age of their mates ($r_s=-0.091$, $P=0.489$, $n=60$).

3.2. Clutch volume

Clutch volume tended to increase with female body mass and was also related to laying date, early clutches being of smaller volume than later clutches (body mass: $r=0.252$, $P=0.053$, $n=60$; laying date: $r=0.424$, $P=0.001$, $n=60$) thus, in the following analysis of clutch volume we controlled for female body mass and laying date. The badge sizes of male plovers were

Tab. 1. Standardized coefficients of independent variables from a multiple linear regression model with male badge size as dependent variable ($F_{6,53}=2.429$, $P=0.038$, $R^2=0.216$).

| Independent variable | β | P |
|----------------------|---------|-------|
| Laying date | -0.393 | 0.004 |
| Male tarsus length | 0.066 | 0.606 |
| Male wing length | 0.120 | 0.365 |
| Female tarsus length | -0.001 | 0.997 |
| Female wing length | -0.031 | 0.807 |
| Female body mass | -0.121 | 0.340 |

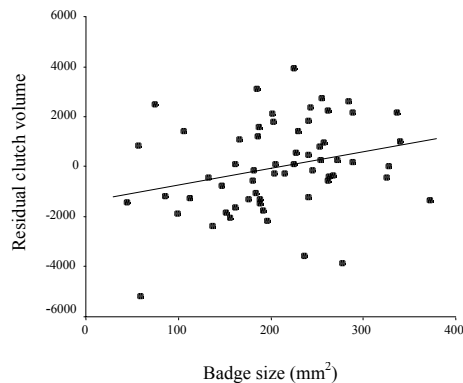


Fig. 2. Relationship between clutch volumes and male badge size ($n=60$ clutches). The residuals of the dependent variable (clutch volume) are calculated from a linear regression model with the following independent variables: laying date, female body mass, female tarsus and wing length, male tarsus and wing length. See text for the details of model selection.

positively associated with the volume of their clutches (Tab. 2., Fig.2.). Other body size measurements of the males and females were unrelated to clutch volumes (Tab. 2.).

4. Discussion

Our study provided two results that may help to understand the adaptive significance of badge size in the Kentish Plover. First, we found that males with early nests have larger badges than males breeding

Tab. 2. Standardized coefficients of independent variables from a multiple linear regression model with clutch volume as dependent variable ($F_{7,52}=3.697$, $P=0.003$, $R^2=0.332$).

| Independent variable | β | P |
|----------------------|---------|---------|
| Laying date | 0.570 | < 0.001 |
| Male badge size | 0.295 | 0.025 |
| Male tarsus length | 0.062 | 0.616 |
| Male wing length | -0.011 | 0.928 |
| Female tarsus length | -0.072 | 0.533 |
| Female wing length | 0.149 | 0.215 |
| Female body mass | 0.236 | 0.052 |

later in the season. At least two alternative explanations can account for this relationship. On the one hand, it is possible that males with larger badges can start breeding earlier than males with small badges, e.g. because large-badged males arrive earlier to the breeding ground, are better in establishing territories, or are more attractive to females. It is unknown for any Kentish Plover population whether arrival of males is related to their badge sizes. In a recent experiment, Lendvai *et al.* (2004) found no evidence for the effect of badge size on remating time of male plovers, but showed that large-badged males may have an advantage in aggressive male-male encounters. Thus, male success in territory establishment may be related to early breeding by large-badged males. If large-badged males can breed early in the season this may increase their reproductive success relative to small-badged males, because nest predation is lower and offspring survival is higher in early Kentish Plover nests than later in the season (Fraga & Amat 1996, Székely & Cuthill 1999). On the other hand, seasonal decline in badge size may be explained by the wear of breast feathers during the season, a fact demonstrated in several bird species (e.g. Bogliani & Brangi 1990). We cannot rule out this latter explanation, although a recent study of Kentish Plovers' breast feather length suggests that this would require significantly quicker abrasion in males than females (Kis & Székely 2003).

As the second main result, we showed that the badge size of males was related to the volume of their clutches. This relationship cannot be explained by a coincidence of seasonal variation in both clutch volume and badge size, because (1) the direc-

tion of seasonal changes in these variables was the opposite and (2) we statistically controlled for seasonal effects. In the sexual selection framework, this result may be explained by several hypotheses.

First, large-badged males may get 'better-quality' mates who are able to increase their parental investment and produce larger eggs (the 'mate quality hypothesis'). Second, it is possible that females of large-badged males could lay larger eggs, because large-badged males may acquire better territories with richer food supplies where their mates may have favourable nutritional conditions. However, both of these explanations are unlikely because neither female body size, body mass nor the minimum age of females were related to their mates' badge size. Third, large-badged males may be better able to defend their mate against harassment of other males, so their females may spend more time feeding, may feed more efficiently, or may avoid detrimental hormonal consequences of frequent fighting. For instance, it has been shown that female Kentish Plovers produce larger eggs when they are in good condition (Amat *et al.* 2001b). Alternatively, repeated aggressive interactions may increase the female's testosterone level, which may have deleterious effect on egg formation and hatching success (*e.g.* Mazuc *et al.* 2003). Finally, it is possible that females preferentially invest in their eggs when paired to a large-badged male (the 'preferential allocation hypothesis'). Our observation seems to support the latter hypothesis, since the relationship between clutch volume and badge size was significant after controlling for female condition (body size and body mass). In line with our result, recent experimental studies of 'cryptic female

choice' revealed that in some birds females lay larger eggs for attractive males than for less preferred mates (*e.g.* Cunningham & Russell 2000). Note, however, that following an experimental manipulation of badge size, new mates of male Kentish Plovers with enlarged badges did not lay larger eggs than new mates of males with control badge size (Lendvai *et al.* 2004). Several explanations can account for the difference between the observational and experimental results. First, in the present observation much larger sample sizes were used than in the experiment to investigate the relationship between badge size and clutch volume (this study: $n=60$, experiment: $n=23$). Second, it is possible that the badge manipulations produced somehow 'unnatural' traits and the females used other cues to assess male quality (Lendvai *et al.* 2004).

Increased clutch volume in large-badged males' nests may significantly influence their reproductive success. For instance, clutch volume is related to brood survival in several precocial birds including the Northern Lapwing *Vanellus vanellus* (Galbraith 1988), the Whimbrel *Numenius phaeopus* (Grant 1991) and the Lesser Scaup *Aythya affinis* (Dawson & Clark 1996; but see also Williams 1994). In the Kentish Plover, within-clutch comparisons showed that chicks hatching from larger eggs were heavier than chicks from small eggs (Amat *et al.* 2001a). Furthermore, chicks hatched from larger eggs were more likely to recruit to the breeding population than their siblings hatched from smaller eggs (Amat *et al.* 2001a). Thus our results suggest that large-badged male Kentish Plovers may have a reproductive advantage over small-badged conspecifics. However, we should

suggest some caution with this interpretation of our results, because we had observations from only one year. Since breeding conditions may differ in many important respects between years (*e.g.* seasonal variation in clutch volumes differs between years in the Kentish Plover; Amat *et al.* 2001a, T. Székely pers. com.), data from several years or more breeding populations would be very valuable to corroborate the conclusion of this study.

Taken together, this study suggests that the badge size of male Kentish Plovers may be affected by sexual selection. The relationship between male badge size and clutch volume can be explained by increased female investment and/or increased success of large-badged males in male-male competition. Further studies are needed to separate the effects of inter- and intrasexual selection.

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Összefoglalás

A hím széki lilék begycsík méretének kapcsolata a fészekalj térfogattal

A partimadarak melanin alapú begymintázatában igen nagy a változatosság a fajok között, de ezen bélyegek adaptív értéke jórészt ismeretlen. A jelen vizsgálatban arra a kérdésre kerestük a választ, hogy a hím széki lilék (*Charadrius alexandrinus*) begycsíkjának változatossága összefügg-e költésük kezdetének időpontjával és fészekaljuk térfogatával. Vizsgálatunkban azt találtuk, hogy a nagyobb begycsikkel rendelkező hímek hamarabb kezdtek költetni, mint a kisebb begycsíkú hímek. A szezonális hatásra történt kontrollálás után összefüggést találtunk a begycsík mérete és a fészekalj össztérfogata között: a nagy begycsíkú hímek fészekaljának térfogata nagyobb volt, mint a kisebb begycsíkú hímeké. Ezek az eredmények arra utalnak, hogy a nagy begycsikkel rendelkező hímek reprodukív előnyben vannak a kisebb begycsíkú hímekkel szemben, mivel a partimadaraknál a korai költés és a nagy tojásméret is növelheti a szaporodási sikert. Mindezek arra engednek következtetni, hogy a begycsík a hímek minőségét jelző bélyeg, mely szerepet játszik a tojók preferenciális befektetésében vagy befolyásolja a hímek sikerét territóriumuk védelme során.

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