Does the expression of a male plumage trait in female Kentish plovers (*Charadrius alexandrinus*) signal individual quality?

Abstract A small percentage (4.5%) of females Kentish plovers (*Charadrius alexandrinus*) observed breeding in southern Spain expressed a plumage trait characteristic of males: the forecrown (frontal) black bar. The expression of this male trait may be age-related, and reversible, i.e., within individuals it may be present in some years but not in other years. Females with frontal bars were not in better condition and nor did they initiate breeding earlier than in years when they lacked frontal bars. Nevertheless, when females had frontal bars they laid larger eggs. I suggest that the frontal bar on females could be an epiphenomenon resulting from hormonal imbalances of females as they age.

Keywords *Charadrius alexandrinus* | Egg size | Individual quality | Sexual trait

Introduction

The expression of secondary sexual traits, such as bright plumage colours or plumage characters, may show individual variation that signals differences in individual quality (Andersson 1994). Some studies have reported the occurrence of females with male-like traits in species with sexual plumage dimorphism. These observations are interesting because they may provide information on the proximate control of plumage dichromatism (Kimball and Ligon 1999), as well as on the function of plumage traits. To explain the expression of male traits in females both functional and

non-functional hypotheses have been proposed. The former have been related to sexual selection, or honest or deceptive signaling (Muma and Weatherhead 1989; Amundsen 2000; Galan 2000; Hockham and Ritchie 2000; Shine et al. 2001; Muller and Wrangham 2002). Non-functional hypotheses have proposed that the expression of male traits in females is due to age-related hormonal imbalances or genetic correlation between the sexes (Lande 1987; Muma and Weatherhead 1989; Swennen et al. 1989; Potti 1993; Hagelin and Kimball 1997; Tella et al. 1997).

Many *Charadrius* species exhibit a conspicuous black frontal (forecrown) bar that may function to signal social status (Graul 1973; Lendvai et al. 2004). In the case of Kentish plovers (*Charadrius alexandrinus*), the males, but not the females, have such a black frontal bar (Cramp and Simmons 1983), and males with larger frontal bars mate earlier (Amat et al. 1999), suggesting that frontal bars may be a sexually selected trait. However, during a study on the breeding biology of the Kentish plover, I found some females with frontal bars. In this paper, I test whether the occurrence of the frontal bars in females is related to their individual qualities, and whether those females with frontal bars have some advantage over those that do not express this plumage trait. If so, I would expect that in years when females exhibit frontal bars they should nest earlier, lay larger eggs, and/or be in better body condition than in other years when the same individuals have no frontal bars.

Methods

The study was conducted at Fuente de Piedra lake in southern Spain, described in Amat et al. (1999). The breeding biology of Kentish plovers was monitored during 1991–1999. For the purposes of this study, I only considered the first nest of each season for each individual, i.e., renesting and second (polygamous) nests were excluded. I compared laying dates and egg volumes of individual females during years in which they had the

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frontal bars and years in which they lacked them. Laying dates of individual females and estimation of egg volumes were determined as indicated in Amat et al. (1999, 2001). Egg sizes were not recorded in 1997–1999. Laying dates were ordered relative to the laying date of the first nest every season. Thus, the laying date of the first nest each year was 1.

Birds were captured at nests using walk-in traps and were individually marked with metal and colour rings. Upon capture, I recorded whether females had a frontal bar. Additional information on the presence of frontal bars on individually colour-ringed females was recorded by observing them with a spotting scope. Females with male-like plumage could be sexed in the hand because incubating Kentish plover females have larger cloacal protuberances than males (personal observation). The body masses were recorded, and the length and width at the centre of the frontal bars were measured as indicated in Amat et al. (1999). Because the females were captured at different stages of incubation, changes in body masses during incubation would affect the reliability of the comparisons. However, at Fuente de Piedra there were no significant changes in body masses of female Kentish plovers during incubation (Amat et al. 2000).

To know whether there were interannual variations in laying dates, egg volumes, and body masses in females that never developed frontal bars, I chose at random six females that had been captured in multiple years and that in none of those years had frontal bars, and assigned at random the years in which such females were captured to two groups. I chose this number of females because I had this kind of data for a similar number of females with frontal bars. Comparisons were then made between the two groups of years.

To test whether the expression of the frontal bar was an age-dependent trait, I scored the years of capture of each individual (1 = first year in which an individual was captured). I then calculated the average scores in years when every individual exhibited the bar, as well as the average scores of years when they had no bars. A comparison of both averages was made using the Wilcoxon signed ranks test (Siegel and Castellan 1988) to examine whether the expression of a frontal bar was more frequent in the later than in the earlier years in which females were captured. For this comparison, I included only those females that were captured in at least 3 years, and females that over the years exhibited both presence and absence of frontal bars (i.e., females that always had a frontal bar were not included). There were eight females that met these two criteria.

Egg volumes were averaged for the entire clutch, so that sample sizes refer to clutches, not to eggs. Comparison of mean values was done with tests for matched pairs, either parametric or non-parametric depending on the type of data. Because some females were captured on multiple occasions, there might be several observations for an individual in a category, in which case I averaged the data for the corresponding category. Sample sizes may differ in different analyses because all information

was not gathered for all individuals in all years. Mean values are presented ± 1 SD.

Results

The occurrence of females with frontal bars was low at the population level. It was recorded in only 16 females (4.5%) out of 358 captured during the study. The length of the frontal bars was similar in females (15.2 ± 1.43 mm, $n=3$) and males (14.3 ± 2.20 mm, $n=274$). The width of the bars at the centre was slightly larger in males (5.0 ± 1.26 , $n=274$) than in females (3.3 ± 1.33 , $n=3$). Qualitatively, the bars of females appeared duller than those of males.

The expression of the frontal bar in female Kentish plovers was a reversible trait. In fact, 33% of individuals captured in multiple years ($n=12$) showed switches in frontal bar expression (Table 1). A Wilcoxon signed ranks test on the scores of years in which females were captured (see Methods) indicated that the expression of the frontal bar was more frequent in the later years in which a given female was captured than in the earlier ones ($P<0.03$). Therefore, the expression of the bar in females was more likely to occur as females aged.

I did not find differences in the laying dates of females in years when they lack frontal bars (47.3 ± 34.17 days from initiation of the first nest in the season) and years in which the same individuals had frontal bars (46.3 ± 24.07 , $n=6$) (Wilcoxon matched-pairs test, $z=0.41$, $P=0.686$). Similarly, in females that never had frontal bars, there were no variations in laying dates between two groups of years (46.2 ± 22.85 vs 31.3 ± 29.56 , $n=6$; Wilcoxon matched-pairs test, $z=1.36$, $P=0.173$).

Mean egg volume was larger when females had frontal bars (8.8 ± 0.21 cm³) than when they have not frontal bars (8.6 ± 0.31 cm³, $n=6$) (Student paired t-test, $t=3.37$, $df=5$, $P=0.020$). However, in females that never expressed frontal bars, there were no differences in egg volumes between two groups of years (9.1 ± 0.58 vs 9.1 ± 0.64 cm³, $n=6$; paired $t=0.27$, $df=5$, $P=0.800$).

I found no differences in body mass of individual females between the years in which they had the frontal bars (41.1 ± 1.59 g) and other years when they have not frontal bars (42.5 ± 3.09 g, $n=7$) (paired $t=1.21$, $df=6$, $P=0.271$). Similarly, there were no differences between two groups of years in body masses of females that never expressed frontal bars (43.1 ± 5.12 vs 42.8 ± 2.23 g, $n=6$; paired $t=0.20$, $df=5$, $P=0.848$).

Discussion

The expression of a frontal bar in female Kentish plovers seemed to be age-related. Also, in other species, the expression of male-like plumages in females is partly age-related and has been assumed to be linked to imbalances of sex hormones (Muma and Weatherhead

Table 1 Occurrence of frontal bars in 16 individual female Kentish plovers (*Charadrius alexandrinus*) during 1991–1999 in Fuente de Piedra lake

Female	1991	1992	1993	1994	1995	1996	1997	1998	1999
ARR	—	—	—	—	—	+	0	0	0
AVR	—	—	0	—	—	0	+	0	0
AYB1	0	0	0	0	0	+	—	0	0
BAN2	0	0	0	0	0	0	+	0	+
BYB1	0	0	0	0	0	+	0	+	+
CJB1	0	0	0	0	+	—	—	0	0
CRA1	0	0	0	0	—	—	0	+	0
JCY1	0	0	0	0	0	—	0	0	+
NRY	0	—	—	+	0	0	0	0	0
RAB1	0	0	—	+	0	—	+	0	0
RAY	0	—	—	0	+	0	0	0	0
RCR2	0	0	0	0	0	0	0	0	+
RCJ2	0	0	0	0	0	0	0	0	+
RJA2	0	0	0	0	0	0	0	0	+
RRA	—	—	—	+	—	+	0	0	0
VRB2	0	0	0	0	0	0	0	0	+

“+” indicates occurrence of the frontal (forecrown) bar, “—” indicates that the female have not a frontal bar, and “0” indicates that the bird was not recorded in the corresponding year

1989; Swennen et al. 1989; Potti 1993; Hagelin and Kimball 1997; Tella et al. 1997; Hegelbach 1998). As in other studies, I also found that the expression of the male trait in females was reversible (Muma and Weatherhead 1989; Tella et al. 1996, 1997; Lank et al. 1999; Potti 1993).

Individual Kentish plover females with frontal bars were not in better body condition, nor did they start laying earlier than when they lacked frontal bars, as was also found in other studies (Potti 1993; Tella et al. 1997). However, females laid larger eggs when they had frontal bars, and this may be advantageous because Kentish plover chicks hatched from larger eggs survive better (Amat et al. 2001). Egg-size in the Kentish plover in Fuente de Piedra lake is not affected by females' age (J.A. Amat, unpublished), and there were no interannual differences in egg-sizes in females that never exhibited frontal bars. Therefore, egg-sizes of females with frontal bars were probably affected by some factor related to the expression of the frontal bar.

The expression of ornamented plumage traits in shorebirds is testosterone-dependent (Kimball and Ligon 1999). Kentish plovers have a partial moult, involving head and body, during the pre-breeding period (December–March) (Cramp and Simmons 1983). If female Kentish plovers have high circulating levels of testosterone during this period, they could express the frontal bar. Because the expression of the bar was apparently more frequent as females became older, the occurrence of the frontal bar could have been caused by age-related hormonal imbalances.

Testosterone levels in eggs of some bird species are positively correlated with testosterone levels in females during egg formation (Schwabl 1996; Gil 2003). Large eggs may have higher levels of androgens than small eggs (Reed and Vleck 2001). If so, the laying of larger eggs by female Kentish plovers with frontal bars would be an epiphenomenon resulting from these females

having higher circulating levels of testosterone. Although increased egg-size may confer some fitness benefits (Amat et al. 2001), increasing circulating androgens levels may be detrimental to females (Reed and Vleck 2001).

Zusammenfassung

Signalisiert das Auftreten eines männlichen Gefieder-Merkmals bei weiblichen Seeregenpfeifern (*C. alexandrinus*) individuelle Qualität?

Ein kleiner Prozentsatz (4.5%) von im südlichen Spanien beobachteten, brutenden weiblichen Seeregenpfeifern entwickelte ein Gefieder-Merkmal, das charakteristisch ist für Männchen: der schwarze Stirnstreifen. Das Ausbilden dieses männlichen Kennzeichens konnte altersabhängig sein und ist umkehrbar, d.h. innerhalb eines Individuums kann es in einigen Jahren vorhanden sein, aber in anderen nicht. Weibchen mit Stirnstreifen waren weder in einer besseren Verfassung, noch begannen sie früher mit Bruten als in anderen Jahren, in denen sie selbst keinen Stirnstreifen hatten. Nichtsdestotrotz legten die Weibchen größere Eier, wenn sie einen Stirnstreifen hatten, als wenn sie keinen hatten. Ich schlage vor, dass der Stirnstreifen bei Weibchen ein Epiphanomen sein konnte, das eine Folge ist von einem hormonellen Ungleichgewicht der Weibchen beim Altern.

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