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The function of female and male ornaments in the Inca Tern: evidence for links between ornament expression and both adult condition and reproductive performance

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Inca Terns *Larosterna inca* are medium-size seabirds that breed along the Peruvian and Chilean coast. They are monogamous and both sexes incubate and contribute to chick provisioning. The sexes are similar in appearance and have elaborate ornaments, including a long white moustache of feathers and fleshy yellow wattles. In this paper we report the differences in ornamentation between sexes and examine whether the trait predicts body condition, reproductive performance or chick quality in either sex. The ornaments were similar in size and coloration between the sexes, except for the wattle length, the difference in which can be due to greater head length in males. Moustache length was the most reliable signal of body condition in both sexes. Moreover, there was a significant relationship between the moustache length and reproductive category of adults (non-breeder, unsuccessful breeder, or one or two chicks fledged). Both asymptotic chick body mass and the T-cell mediated response of chicks (a measure of immunocompetence) were related to the moustache length of male and female adults. These results provide support for the role of ornaments in mutual signalling of condition in this species. Female and male ornaments predict body condition, reproductive performance and chick quality, as predicted by sexual selection models.

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In many animal species males have elaborate ornaments, while females are cryptic in appearance. This phenomenon has been attributed to sexual selection acting primarily on the male sex (review in Andersson 1994). Females paired with attractive males may gain either direct benefits such as territorial resources, parental care and the avoidance of infectious diseases (Kirkpatrick and Ryan 1991), or indirect benefits derived from attractive offspring (Fisher 1930), and even enhance the viability of their offspring by selecting traits that indicate male genetic quality (Zahavi 1975, Hamilton and Zuk 1982, Kodric-Brown and Brown 1984, Grafen 1990). Females can assess the variation in male quality if males in better condition express more elaborate display. The idea that male ornaments indicate condition is supported by studies showing that the expression of ornaments correlates with adult condition and survival (Andersson 1994). Male ornaments may also be related to intrasexual selection because they signal male dominance status (Järvi and Bakken 1984, Evans and Hatchwell 1992).

However, females of several species show some expression of the same ornaments as males. Two main hypotheses have been proposed to explain this. The 'correlated response hypothesis' posits that female ornaments are themselves selectively neutral or even detrimental, but result from a genetic correlation between the trait in males and females in combination with the selection for the trait in males (Lande 1980, Muma and Weatherhead 1989, Hill 1993, Cuervo et al. 1996, Tella et al. 1997). The 'direct selection hypothesis' suggests that female ornaments are themselves under selection, either through female-female competition or male choice (Darwin 1871, Jones and Hunter 1999, Amundsen 2000). Also female ornaments may signal social dominance in contests over limited resources, such as territories or mates (West-Eberhard 1983, Irwin 1994). Moreover, they may indicate reproductive or genetic quality, and hence are preferred by choosy males (Jones and Montgomerie 1992, Johnsen et al. 1996, Potti and Merino 1996, Amundsen et al. 1997, Linville et al. 1998, but see Hill 1993). Thus, similar preferences for ornaments in both sexes and similar competition within both sexes can explain ornament monomorphism in some bird species (Jones and Hunter 1999).

Mutual sexual preference is expected to occur in species where members of both sexes benefit from obtaining the highest quality mate, such as those where males provide a substantial amount of parental care to the offspring (Trivers 1972, Johnstone et al. 1996). In the Crested Auklet *Aethia cristatella*, a seabird with monomorphic ornaments, both sexes showed a preference for models with experimentally enlarged crests (Jones and Hunter 1993). Selection for mutual signalling of condition is generally expected in seabirds, because they breed in dense colonies (thus offering considerable potential for exercising choice), and both sexes make large contributions to rearing the offspring and vary substantially in quality (Johnstone et al. 1996). Within both sexes competition can be intense in seabird species, so intrasexual selection within sexes could focus on ornaments that function in competition for access to mates (Jones and Hunter 1999).

Inca Terns *Larosterna inca* are medium-size seabirds (c. 220 g) that breed in burrows on talus slopes and cliffs along the Peruvian and Chilean coast (Guillen 1988). They feed in large flocks on anchovies *Engraulis ringens* in the Humboldt current system (Murphy 1936), and under stable conditions rear two broods in a year. They are monogamous, pair-formation occurs every season in the communal areas, and both sexes incubate and contribute to chick provisioning (Moynihan 1962, Velando unpubl. data). In other tern species, the total parental expenditure by males is equal to or outweighs that of females (Fasola and Saino 1995) and the divorce rate is very high (c. 58% in Caspian Terns *Sterna caspia*, Cuthbert 1985). In Inca Terns the sexes are similar in appearance, both displaying elaborate ornaments including a long white moustache of feathers and fleshy yellow wattles. The ornaments are displayed during the whole year and could be a reliable signal of quality in both sexes. In this paper we quantified differences in ornamentation between sexes and examined whether ornaments predicted body condition, reproductive performance or chick quality in either sex, as predicted by some sexual selection hypotheses.

Methods

Study area and studied animals

This study was carried out on the Isla La Vieja, Reserva Nacional de Paracas, Peru (14°17′S, 76°11′W), from October to December 1999. Inca Terns build their nests in crevices in cliffs along the coast of the island and lay one, or more frequently two eggs. We marked 90 nests in three adjacent sub-colonies during the laying period. Hatching order and date of hatching of each chick in the brood were obtained by making daily visits around the time of hatching. Each chick was tagged with a coloured velcro strip around the tarsus that identified chicks within brood. These strips were expanded as the chicks grew. Hatching dates provided an indication of laying date. The reproductive success of each nest was recorded as the number of chicks fledged.

During incubation, we captured adults at the nest at night. To reduce the risk of desertion, we only caught one adult per nest. Therefore, we could not investigate assortative mating for ornament size or control for the ornament size of the other adult in the analysis of reproductive category. During the same period, we also captured 16 non-breeding adults by night-lighting at a roost away from the colonies. Birds were weighed to the nearest gram using a spring balance. We measured head length (to the nearest 0.01 mm) with digital callipers and wing length (to the nearest mm) with a metal ruler with a stop. A blood sample was obtained from each bird by puncturing the brachial vein and transferring the blood to a tube containing an equal volume of ethanol. Sex was determined through PCR amplification of part of the CHD gene using primers P2 and P8 following Griffiths et al. (1998). PCR products were visualized and photographed under UV light. As expected, two patterns were observed, one consisting of a single band of approximately 390 bp, corresponding to males, and the other showing a second additional band of approximately 420 bp, corresponding to females. Sex determined in this way agreed with that based on behaviour for two females and two males.

Ornament measurements

Inca Terns have slate-coloured plumage and a crimson bill and legs. They are ornamented with long white feather moustaches and yellow gape wattles (Fig. 1). The moustaches consist of tufts of white feathers on either side of the head running from in front of the eyes to the back of the cheeks, where they are prolonged by the plumes of the feathers. We measured the length of the straightened left and right moustaches of captured individuals (to the nearest mm) using a transparent ruler (see Fig. 1). Moustache length was the mean of these two values, and moustache asymmetry their absolute difference. The right wattle length was measured (to the nearest 0.01 mm) with digital callipers. The colour of wattles was scored by comparison with a commercial PANTONE® S-5 colour card from 1 (dull orange) to 5 (bright yellow). Birds have a UV-sensitive vision, and therefore they can perceive colour signals not perceived by humans (Bennet and Cuthill 1994). This could be a potential problem for this study because we did not measure UV-light reflection. Therefore in this study we may have mis-measured UV colour; however, it has been argued that quantifying coloration exclusively by human retina can be reasonable for longer wavelengths (Zuk and Decruyenaere 1994, Andersson 1999).

Adult condition

We studied the relationships between adult body condition and ornament expression. In our sample there was no relationship between body mass and the number of days between laying and capture dates, so body mass was not corrected for this variable. In order to avoid the effect of body size on body condition, we estimated body condition using residuals from the regression of body mass (in g) on head length (in mm) for males and females separately (Females: body mass = 4.19 (head length) − 135.89, $r^2 = 0.19$, $n = 61$, $p < 0.001$, Males: body mass = 4.53 (head length) − 170.91, $r^2 = 0.13$, $n = 43$, $p = 0.01$). The residuals were standardized within each sex. We also carried out the analysis using body mass and the residual of body mass on wing length (body mass = 1.01 (wing length) − 64.23, $r^2 = 0.12$, $n = 106$, $p < 0.001$) as indicators of body condition.

Chick growth and immunocompetence

Asymptotic chick body mass was measured at 25–30 days old using a spring balance (to the nearest gram). As a measure of immunocompetence, we used the T-cell-mediated immune response to an injection of 0.1 mg of phytohaemaglutinin (PHA) in 0.05 ml of phosphate buffered saline (PBS) in the left wing web (Smiths et al. 1999). The point of injection was marked with an indelible marker. Three replicate measurements of patagium thickness were taken with a digital micrometer to the nearest 0.001 mm prior to the injection, and again 24 h later. The 'wing web index' was the change in thickness (mm) of the wing web (difference between 24-h post-injection thickness and pre-injection thickness). The repeatability of wing-web measurements was derived from the intra-class correlation coefficient (Lessells and Boag 1987). Wing-web thickness measures were significantly repeatable, both for initial measures ($r = 0.916$, $F_{58,110} = 33.65$, $p < 0.0001$) and for final measures ($r = 0.959$, $F_{50,102} = 70.48$, $p < 0.0001$). Asymptotic chick body mass and wing web index were not related with chick order, brood size or nestling age, so they were not corrected for these variables.

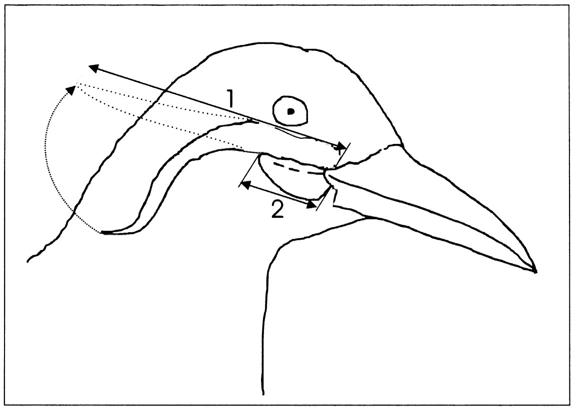

Fig. 1. Measurement of Inca Tern ornaments (see Methods). 1. Moustache length, measured to the tip of the longest plume when the moustache was straightened. 2. Wattle length, measured as the maximum length of the fleshy wattles.

Results

Differences between sexes

The mean ornament sizes of adult birds caught during incubation and sexed by molecular analysis are given in Table 1. No sexual differences were found in moustache length, moustache asymmetry and wattle colour. Wattle length was slightly but significantly longer in males than in females. Body mass and wing length were similar in the two sexes, but head length was longer in males. Moreover, there was a significant correlation between wattle length and head length ($r = 0.37$, $n = 107$, $p < 0.001$). Thus, the differences between sexes in wattle length could be due to sexual differences in head size.

Relationships among ornament characteristics were investigated using correlation. Moustache length was positively correlated with wattle length ($r = 0.32$, $n = 104$, $p = 0.001$) and wattle colour ($r = 0.29$, $n = 103$ $p = 0.004$). None of the other correlations between ornament measures were significant ($p > 0.05$).

Ornamentation and condition of adult birds

Body condition (the residuals of body mass on head size) was related to male and female ornaments (Table 2). Overall, ornaments explained a significant proportion (19%) of the variance in body condition of adult birds. In analyses of covariance examining sexual differences in the relationships between each ornament measure and body condition, none of the sex or interaction terms were significant ($p > 0.05$ in each case).

Table 1. Sexual differences in ornaments (see Fig. 1), body size and body mass of adult Inca Terns sexed by molecular analysis compared by t-tests and Mann-Whitney test. Significant differences are indicated in bold type. Sexual dimorphism index (SDI) is expressed as male mean/female mean.

Trait	Females			Males			Differences		
	Mean	SE	n	Mean	SE	n	SDI	t or Z[a]	p
Head length (mm)	**84.27**	0.20	62	**86.98**	0.22	43	**1.03**	8.85	**0.001**
Wing length (mm)	280.95	0.82	62	281.02	0.65	43	1.00	0.69	0.94
Body mass (g)	216.9	1.94	62	222.91	2.7	43	1.03	1.78	0.08
Moustache length (mm)	70.37	0.56	60	69.67	1.64	42	0.99	0.46	0.65
Moustache asymmetry (mm)	2.03	0.22	60	1.72	0.25	42	0.85	0.83	0.41
Wattle length (mm)	**15.40**	0.13	61	**15.98**	0.17	43	**1.04**	2.63	**0.01**
Wattle colour score[a]	2.47	0.10	61	2.25	0.15	40	0.91	1.15[a]	0.24

[a] Wattle colour scores were tested using a Mann-Whitney test, for which the Z value is given.

Table 2. Correlation coefficients between body condition (residuals from the regression of body mass on head length for each sex) and five ornament measures. The results from multiple regression analyses using all trait measures are also shown. Significant correlations are indicated in bold type.

	Females			Males			Total		
	r	n	p	r	n	p	r	n	p
Moustache length (mm)	**0.40**	60	**0.002**	0.33	42	**0.030**	**0.38**	102	<**0.001**
Moustache asymmetry (mm)	−0.10	60	0.425	−0.20	42	0.200	−0.14	102	0.166
Wattle length (mm)	0.23	61	0.070	**0.29**	42	**0.049**	**0.25**	103	**0.011**
Wattle colour score	**0.32**[a]	61	**0.011**	0.05[a]	42	0.741	0.19[a]	103	0.052
Multiple regression	**0.44**	60	**0.013**	0.43	42	0.080	**0.44**	102	<**0.001**

[a] Spearman rank correlation.

Moustache length was the only ornament to which body condition was significantly related. This variable accounted for 11% of the variance in male body condition and 16% of the variance in female body condition. Similar relationships were found between the residuals of body mass on wing length, or body mass, and moustache length (Fig. 2).

There was a significant relationship between moustache length and reproductive category of both sexes of adults (Fig. 3), but the sex and interaction effects were not significant. A post hoc analysis (LSD) in both sexes combined indicated that successful birds had significantly longer moustaches than non-breeding ones ($p = 0.001$). The residuals of moustache length on body condition (Fig. 2a) were used to control for the effect of body condition on moustache length. Thus, the effect of moustache length on reproductive category after controlling for body condition was also significant ($F_{3,86} = 2.76$, $p = 0.047$). Reproductive category and success (number of young fledged) were not related to any other ornament measure ($p > 0.10$ in each case). Also, there was no relationship between timing of breeding and any ornament ($p > 0.10$ in all cases).

Adult ornamentation and chick condition

We used body mass and wing web index of chicks as indicators of chick quality. These measures were strongly correlated, and therefore nestlings of small body mass had poorer mean immunocompetence than those of large body mass ($r = 0.46$, $n = 27$, $p = 0.01$). Mean chick mass and wing web index were not correlated with parents' body condition (mean chick mass: $r = 0.23$, $n = 33$, $p = 0.20$; mean wing web index: $r = 0.05$, $n = 39$, $p = 0.79$). Only parent moustache length was correlated with mean chick mass and mean wing web index (Fig. 4). In analyses of covariance examining sexual differences in the relationships between moustache length and chick mass or immunocompetence none of the sex or interaction terms were significant ($p > 0.05$ in each case). Thus, both males and females with larger moustaches reared heavier chicks with better immune responses (Fig. 4).

Discussion

The results of this study showed that ornaments provide a good indication of individual quality among adult Inca Terns. Body size, ornament size and coloration were similar in both sexes, except for head and wattle length, which were both longer in males. Moreover, the ornaments provided a similar indication of condition in both sexes (Table 2). Of the ornaments measured, moustache length seemed to most reliably reflect female and male quality: adults with longer

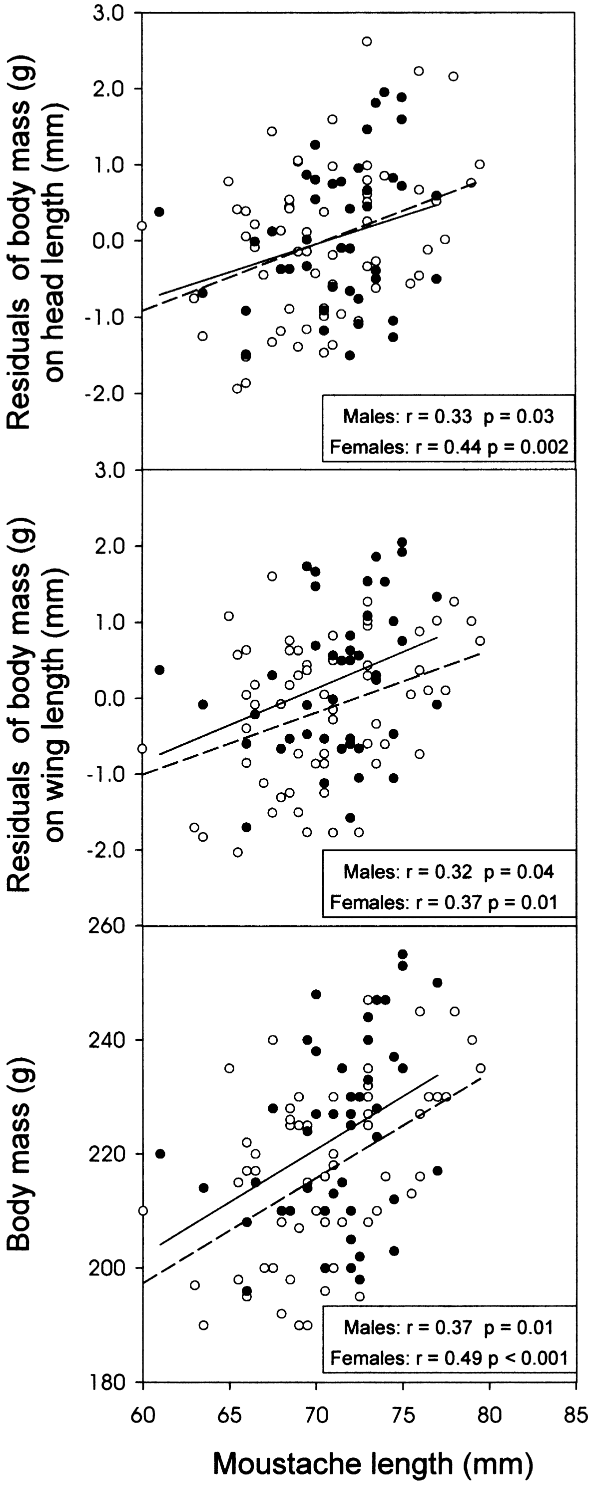

Fig. 2. Relationships between body condition (residuals of body mass on head or wing length) or body mass and moustache length of adult Inca Terns (44 males, ●; and 61 females, ○).

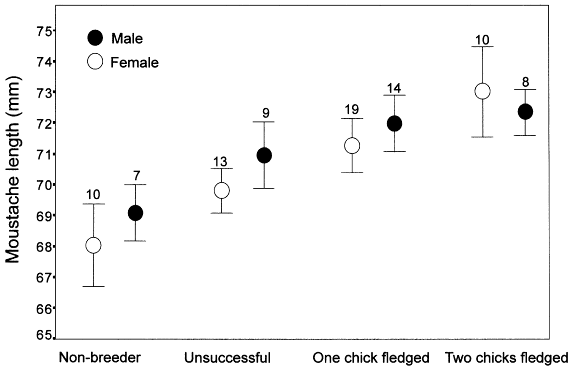

Fig. 3. Moustache length (Mean ± SE) of adult Inca Terns in relation to reproductive category. Numbers above the bars are sample sizes. Because only one adult from each pair was caught, reproductive category is only scored once for each nest. The results of General Linear Model (GLM) were: sex: $F_{1,82} = 0.63$, $p = 0.421$; category: $F_{3,82} = 4.67$, $p = 0.005$; category × sex: $F_{1,82} = 0.34$, $p = 0.797$.

moustaches were the most productive and their chicks were heavier and had better immune responses. These results are consistent with predictions of honest advertisement models (e.g. Kodric-Brown and Brown 1984, Grafen 1990). Nevertheless, correlation between ornaments and condition may also be consistent with other models, such as 'sensory exploitation' (Jones and Hunter 1998) and 'Fisherian runaway' (Balmford and Read 1991, Jones and Hunter 1998). If the ornaments play an important role in signalling, they may be involved in mate choice, in competition among members of the same sex, or in both (Jones and Hunter 1999, Amundsen 2000).

In many bird species, breeding success declines seasonally (review for seabirds in Moreno 1998) and in some of these species, the early breeders are more ornamented (e.g. Järvi et al. 1987, Møller 1994). In our study, we did not find any relationship between adult ornamentation and the timing of breeding. In tropical seabirds, such as Inca Terns, the timing of breeding is irregular and not constrained by seasonal influences (Ashmole 1971, Zavalaga 1997). Thus, a correlation between ornament expression and laying date is not expected in this species. We found a positive relationship between chick mass or immunocompetence and moustache length. However, there was no relationship between chick mass or immunocompetence and adult condition, and the relationship between moustache length and reproductive category was significant also when controlled for body condition. In Inca Tern chicks, immunocompetence was positively correlated with nestling mass. This result agrees with other studies, which have shown a positive relationship between nutritional condition, survival and immunocompetence of nestlings (e.g. Saino et al. 1997, Christe et al. 1998; see also Alonso-Alvarez and Tella 2001). In a cross-fostering experiment, cell-mediated immunity in nestling Great Tits *Parus major* was due to both environmental and heritable variation (Brinkhof et al. 1999). Thus, the correlation between chick mass and immunocompetence and parents' moustache length found in this study could be due to higher genetic and/or phenotypic quality of the adults.

There is some indirect evidence that Inca Tern ornaments are influenced by sexual selection. Both the white moustache and yellow wattle appear only in birds of breeding age. They are prominently emphasized during courtship and hostile displays in both sexes (Moynihan 1962, Velando unpubl. data), but have no obvious use in parental care, foraging or thermoregulation. Thus, the ornaments of Inca Terns may have evolved by sexual selection driven by mating preferences or intrasexual competition.

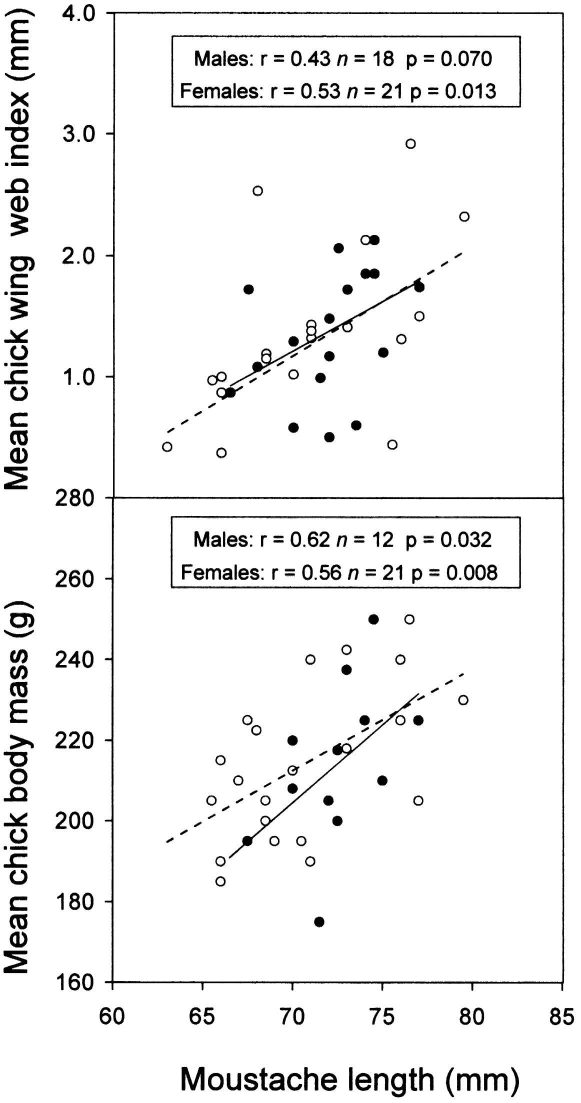

Fig. 4. Mean wing web index and body mass of nestlings in relation to moustache length of adult male (●) and female (○) Inca Terns.

In several species, there is evidence that ornaments are the product of sexual selection, but studies have usually concentrated on male traits (Andersson 1994, but see Jones and Hunter 1993, 1999, Amundsen et al. 1997, Amundsen 2000, Jones et al. 2000). Studies on dimorphic birds, in which the females show some limited expression of the ornaments found in males, have reached mixed conclusions. Some support the correlated response (Johnson 1988, Muma and Weatherhead 1989, Hill 1993, Cuervo et al. 1996, Tella et al. 1997), but others support the direct selection hypothesis (Johnsen et al. 1996, Potti and Merino 1996, Amundsen et al. 1997, Linville et al. 1998, Hansen et al. 1999).

Few studies have investigated ornament expression in females of monomorphic species. In Crested Auklets, a monomorphic seabird, crest size is the product of inter- and intrasexual selection in both sexes (Jones and Hunter 1993, 1999, Jones et al. 2000). In Least Auklets *Aethia pusilla*, another monomorphic species, there is also some evidence for mutual sexual selection (Jones and Montgomerie 1992). Mutual sexual selection (intra- and intersexual selection) is expected in seabirds because the parental roles are similar in males and females (Johnstone et al. 1996, Jones and Hunter 1999) and many seabird species have sexually monomorphic ornaments which are used by both sexes in courtship and hostile displays (e.g. Inca Tern, Moynihan 1962; tropicbirds (Phaethontidae), van Tets 1965; Long-tailed Skua *Stercorarius longicaudus*, Andersson 1971; Crested Auklet, Jones 1993).

Inca Terns are sexually monomorphic in their ornaments (Table 1), and we found a significant relationship between adult condition and ornament expression in both sexes (Figs 2–3). According to the correlated response hypothesis female ornaments have no function, but our results showed a link between female condition or reproductive performance and the expression of female moustaches. However, the relationship between reproductive performance and female ornament could be due to assortative mating with respect to moustache length and a genetic correlation between female expression and female preference for male ornamentation (Cuervo et al. 1996). In this case, moustache length should be a better predictor of quality in males than in females. However, in our study we found equally strong relationships between reproduction, chick mass or immunocompetence and ornaments in females and males. Moreover, the relationship between ornamentation and condition suggests that ornaments may be costly to produce or maintain. If the ornaments are costly, our results agree better with the hypothesis that female traits are themselves under selection. Ornament expression can be limited by the direct cost of producing the ornament itself or by social control and the cost of dominance (Andersson 1994, Jones and Hunter 1999). During the studied season (October to December 1999), the terns had a good breeding season with abundant anchovies, as a consequence of a cold rich phase after the 1997–1998 El Niño. In 1998, Inca Terns did not breed due to low anchovy availability during El Niño (Jahncke 1998). In this year they had shorter moustaches than in 1999, and there was a correlation between moustache length and body condition (explaining 20% of the variance; Velando and Márquez unpubl. data), which suggests a strong relationship between ornament expression and adult condition.

An alternative explanation for the observed relationship between condition and ornament expression, which we did not test, could be that the ornament expression is related to age. Age effects would not allow us to distinguish between correlated and direct hypotheses (Muma and Weatherhead 1989). In conclusion, our results seem to support that ornaments have a signalling function in both sexes of Inca Tern, which is consistent with the hypothesis that female ornaments are directly under selection themselves. However, the correlated response hypothesis cannot be entirely refuted by this study, as we did not test whether the ornaments are used as signals. In addition, this study provides little insight into which, if any, direct selection mechanism best explains female ornament function and evolution. Therefore, experimental studies of this species are required to test the role that ornaments play in signalling parental quality, in mate choice and in intrasexual interactions, particularly in females.

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References

Alonso-Alvarez, C. and Tella, J. L. 2001. Effects of experimental food restriction and body-mass changes on the avian T-cell-mediated immune response. – Can. J. Zool. 79: 101–105.

Amundsen, T. 2000. Why are female birds ornamented? – Trends Ecol. Evol. 15: 149–155.

Amundsen, T., Forsgren, E. and Hansen, L. T. T. 1997. On the function of female ornaments: male bluethroats prefer colourful females. – Proc. R. Soc. Lond. B 264: 1579–1586.

Andersson, M. 1971. Breeding behaviour of the long-tailed skua *Stercorarius longicaudus* (Viellot). – Ornis Scand. 2: 35–54.

Andersson, M. 1994. Sexual Selection. – Princeton Univ. Press, Princeton, New Jersey.

Andersson, S. 1999. Morphology of UV reflectance in a whistling-thrush: implications for the study of structural colour signalling in birds. – J. Avian Biol. 30: 193–204.

Ashmole, N. P. 1971. Seabird ecology and the marine environment. – In: Farner, D. S., King, J. K. and Parkes, K. C. (eds). Avian Biology. Vol. 1. Academic Press, New York, pp. 224–286.

Balmford, A. and Read, A. F. 1991. Testing alternative models of sexual selection through female choice. – Trends Ecol. Evol. 6: 274–276.

Bennet, A. T. D. and Cuthill, I. C. 1994. Utraviolet vision in birds: what is its function? – Vis. Res. 34: 1471–1478.

Brinkhof, M. W. G., Heeb, P., Kölliker, M. and Richner, H. 1999. Immunocompetence of nestling great tits in relation to rearing environment and parentage. – Proc. R. Soc. Lond. B 266: 2315–2322.

Christe, P., Møller, A. P. and de Lope, F. 1998. Immunocompetence and nestling survival in the house martin: the tasty chick hypothesis. – Oikos 83: 175–179.

Cuervo, J. J., de Lope, F. and Møller, A. P. 1996. The function of long tails in female barn swallows (*Hirundo rustica*): an experimental study. – Behav. Ecol. 7: 132–136.

Cuthbert, F. J. 1985. Mate retention in Caspian tern. – Condor 87: 74–78.

Darwin, C. 1871. The Descent of Man, and Selection in Relation to Sex. – John Murray, London.

Evans, M. R. and Hatchwell, B. J. 1992. An experimental study of male adornment in the scarlet-tufted malachite sunbird: I. The role of pectoral tufts in territorial defence. – Behav. Ecol. Sociobiol. 29: 421–427.

Fasola, M. and Saino, N. 1995. Sex-biased parental-care allocation in three tern species (Laridae, Aves). – Can. J. Zool. 73: 1461–1467.

Fisher, R. A. 1930. The Genetical Theory of Natural Selection. – Oxford University Press, London.

Grafen, A. 1990. Sexual selection unhandicapped by the Fisher process. – J. theor. Biol. 144: 473–516.

Griffiths, R., Double, M. C., Orr, K. and Dawson, R. J. G. 1998. A DNA test to sex most birds. – Mol. Ecol. 7: 1071–1075.

Guillen, V. 1988. Variaciones de la población del Zarcillo (*Larosterna inca*: Aves) durante 1963 y 1965 en el litoral peruano, con énfasis en la Isla Asia. – In: Salzwendel, H. and Landa, A. (eds). Recursos y dinámica del ecosistema de afloramiento peruano. Boletín Intituto del Mar del Perú, Volumen extraordinario, Lima, pp. 335–340.

Hamilton, W. D. and Zuk, M. 1982. Heritable true fitness and bright birds: A role for parasites? – Science 218: 384–387.

Hansen, L. T., Amundsen, T. and Forsgren, E. 1999. Symmetry: attractive not only to females. – Proc. R. Soc. Lond. B 266: 1235–1240.

Hill, G. E. 1993. Mate choice and the evolution of female plumage coloration in the House Finch. – Evolution 47: 1515–1525.

Irwin, R. E. 1994. The evolution of plumage dichromatism in the New World blackbirds: social selection on female brightness? – Am. Nat. 144: 890–907.

Jahncke, J. 1998. Las poblaciones de aves gauneras y sus relaciones con la abundancia de anchoveta y la ocurrencia de eventos El Niño en el mar peruano. – Bol. Inst. Mar. Per. 17: 1–13.

Järvi, T. and Bakken, M. 1984. The function of the variation in the breast stripe of the great tit (*Parus major*). – Anim. Behav. 32: 590–596.

Järvi, T., Røskaft, E., Bakken, M. and Zumsteg, B. 1987. Evolution of variation in male secondary sexual characteristics. – Behav. Ecol. Sociobiol. 20: 161–169.

Johnson, K. 1988. Sexual selection in pinyon jays II: male choice and female-female competition. – Anim. Behav. 36: 1038–1047.

Johnsen, T. S., Hengeveld, J. D., Blank, J. L., Yasukawa, K. and Nolan, V. Jr. 1996. Epaulet brightness and condition in female Red-winged Blackbirds. – Auk 113: 356–362.

Johnstone, R. A., Reynolds, J. D. and Deutch, J. C. 1996. Mutual mate choice and sex differences in choosiness. – Evolution 50: 1382–1391.

Jones, I. L. 1993. Crested auklet. – In: Poole, A., Stettenheim, P. and Gill, F. (eds). The Birds of North America. Vol. 70. The Academy of Natural Sciences, Philadelphia, pp. 1–15.

Jones, I. L. and Hunter, F. M. 1993. Mutual sexual selection in a monogamous seabird. – Nature 362: 238–239.

Jones, I. L. and Hunter, F. M. 1998. Heterospecific mating preferences for a feather ornament in least auklets. – Behav. Ecol. 9: 187–192.

Jones, I. L. and Hunter, F. M. 1999. Experimental evidence for mutual inter- and intrasexual selection favouring a crested auklet ornament. – Anim. Behav. 57: 521–528.

Jones, I. L. and Montgomerie, R. 1992. Least auklet ornaments: do they function as quality indicators? – Behav. Ecol. Sociobiol. 30: 43–52.

Jones, I. L., Hunter, F. M. and Fraser, G. 2000. Patterns of variation in ornaments of Crested Auklets *Aethia cristatella*. – J. Avian Biol. 31: 119–127.

Kirkpatrick, M. and Ryan, M. J. 1991. The evolution of mating preferences and the paradox of the lek. – Nature 350: 33–38.

Kodric-Brown, A. and Brown, J. H. 1984. Truth in advertising. The kinds of traits favored by sexual selection. – Am. Nat. 124: 309–323.

Lande, R. 1980. Sexual dimorphism, sexual selection and adaptation in polygenic characters. – Evolution 34: 292–305.

Lessells, C. M. and Boag, P. T. 1987. Unrepeatable repeatabilities: a common mistake. – Auk 104: 116–121.

Linville, S. U., Breitwish, R. and Schilling, A. J. 1998. Plumage brightness as an indicator of parental care in northern cardinals. – Anim. Behav. 55: 119–127.

Møller, A. P. 1994. Sexual Selection and the Barn Swallow. – Oxford Univ. Press, Oxford.

Moreno, J. 1998. The determination of seasonal declines in breeding success in seabirds. – Etología 6: 17–31.

Moynihan, M. 1962. Hostile and sexual behavior patterns of South American and Pacific Laridae. – E.J. Brill, Leiden.

Muma, K. E. and Weatherhead, P. J. 1989. Male traits expressed in females: Direct or indirect sexual selection? – Behav. Ecol. Sociobiol. 25: 23–31.

Murphy, R. C. 1936. Oceanic Birds of South America. Vol. 2. – Mcmillan, New York.

Potti, J. and Merino, S. 1996. Decreased levels of blood trypanosome infection correlate with female expression of a male secondary sexual trait: implications for sexual selection. – Proc. R. Soc. Lond. B 263: 1199–1204.

Saino, N., Calza, S. and Møller, A. P. 1997. Immunocompetence of nestling barn swallows in relation to brood size and parental effort. – J. Anim. Ecol. 66: 827–836.

Smiths, J. E., Bortolotti, G. R. and Tella, J. L. 1999. Simplifying the phytohemaglutinin skin testing technique in studies of avian immunocompetence. – Funct. Ecol. 13: 567–577.

Tella, J. L., Forero, M. G., Donázar, J. A. and Hiraldo, F. 1997. Is the expression of male traits in female Lesser Kestrels related to sexual selection? – Ethology 103: 72–81.

Trivers, R. L. 1972. Parental investment and sexual selection. – In: Campbell, B. (ed). Sexual Selection and the Descent of Man 1871–1971. Aldine, Chicago, pp. 136–179.

van Tets, G. F. 1965. A comparative study of some social communication patterns in the Pelecaniformes. – Ornithol. Monogr. 2: 1–88.

West-Eberhard, M. J. 1983. Sexual selection, social competition, and speciation. – Q. Rev. Biol. 55: 155–183.

Zahavi, A. 1975. Mate selection – a selection for a handicap. – J. theor. Biol. 67: 205–214.

Zavalaga, C. 1997. Ecología reproductiva del Zarcillo (*Larosterna inca*, Lesson) en Punta San Juan, Perú. – Tesis de Licenciatura, Universidad Peruana Cayetano Heredia, Lima.

Zuk, M. and Decruyenaere, J. G. 1994. Measuring individual variation in colour – a comparison of two techniques. – Biol. J. Linn. Soc. 53: 165–173.

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