

PLUME VARIATION, BREEDING PERFORMANCE AND EXTRA-PAIR COPULATIONS IN THE CATTLE EGRET

by

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Summary

We investigate how variation in breeding plumes influences pairing patterns, extra-pair copulations and breeding performance in the colonial cattle egret (*Bubulcus ibis ibis*). The breeding plumes of both male and female cattle egrets varied from almost none, to lush head, back and scapular plumes. Overall, male breeding plumes were longer and darker than those of females, but we observed the full range of plume development in both sexes. Plume development was positively correlated within breeding pairs. Females may be more selective in mate choice since they only paired with males with similar or better plumes and only accepted extra-pair copulations when the male had plumes that were greater than or equal to those of their mates. Males, in contrast frequently paired with females of lower plume development, and did not target well plumed females for extra pair copulations. Females may obtain direct benefits from pairing with well plumed males since these males copulated and fed chicks at a higher rate, although this did not lead to higher fledging success in our study. Well plumed females did not have higher nest attendance, nestling attendance, feeding rates or fledging

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success. Nevertheless, males appeared to invest more in a breeding attempt when paired to a well plumed female by increasing copulation rates, mate attendance and nest site attendance. Breeding plumes may therefore signal both parental and genetic quality to prospective mates.

Keywords: sexual selection, mate choice, monogamy, parental care, ornamentation, extra-pair copulations.

Introduction

Female mating preferences can lead to the evolution of elaborate ornaments in males via sexual selection (Darwin, 1871; Andersson, 1994). In birds, females mate preferentially with males bearing more elaborate ornaments (e.g. peacocks *Pavo cristatus*, Petrie et al., 1991; Petrie & Halliday, 1994), brighter colours (e.g. house finches *Carpodacus mexicanus*, Hill, 1991) or better displays (e.g. satin bowerbirds *Ptilonorhynchus violaceus*, Borgia, 1985). Females may mate with males based on specific physical or behavioural attributes if they obtain an immediate benefit such as access to food or higher levels of subsequent parental care (Heywood, 1989; Hoelzer, 1989). Alternatively, females may mate with certain males if they obtain indirect genetic benefits that increase offspring fitness (Andersson, 1994). Male traits may signal genetic benefits by virtue of being correlated with viability (e.g. Trivers, 1972; Zahavi, 1975; see Andersson, 1994, for a review), or they may be arbitrary traits that reflect male attractiveness in mating (Fisher, 1915, 1930).

Although sexual selection will be most intense in societies with high variance in mating success, elaborate traits appear to be maintained by mating preferences even in socially monogamous species. Females in some monogamous species prefer to

Since females benefit from male parental care, it is difficult in monogamous species to distinguish mating preferences for material benefits from those for genetic benefits. In some species apparent preferences for both have been demonstrated. In great tits (*Parus major*) females preferred to pair with males with large chest stripes and benefited directly since chest stripe size was correlated with several aspects of male parental care (Norris, 1990a, b, 1993), but subsequent cross-fostering experiments demonstrated that the preferred trait may also be correlated with the genetic quality of males, since males with large stripes survived better (Norris, 1993). Thus female great tits apparently benefited by selecting a trait that simultaneously signalled material and genetic benefits.

In socially monogamous species, comparisons of within pair and extra-pair mating preferences may allow the relative importance of direct and indirect benefits to be assessed. If more ornamented birds provide more parental care, an individual will obtain direct benefits by pairing with a better ornamented mate, but if these birds are also preferred during extra-pair copulations, this suggests that the trait also signals underlying genetic benefits. We investigate the function of breeding plumes in the socially monogamous cattle egret (*Bubulcus ibis ibis*). During the breeding season both sexes of cattle egrets develop lush filamentous plumes. The breeding plumes of

pairs in a small sub-section of the colony. The colony was located in a large bearded fig tree (*Ficus citrifolia*) in a deep gully, so we were able to sit relatively close to the colony (10-30 m away) in a paddock above the gully and observe pairs without disturbing the colony. We were able to recognize pairs in this subsection of the colony using the stage of breeding, individual plume development, idiosyncrasies of the plumage or face, and the position

TABLE 1. Scoring system used to assign plume scores to breeding plumes on the head, chest and back of individual

lateral wipes and cloacal contact was unlikely to have occurred. If the male fell off the back of the female, or if the female was unable to remain on the branch, a copulation was also categorised as unsuccessful.

Intra-pair copulations usually occurred when one member of the pair returned to the nest. Typically, a pair would greet and 'backbite' (Blaker, 1969), and the returning bird would preen or nestbuild for several minutes before a copulation occurred. Within pairs, females occasionally solicited males, but often the male climbed on the back of the female with no solicitation and began treading. After intra-pair copulations, the male usually remained in the area, preening near the nest while the female engaged in nestbuilding activity.

In contrast, extra-pair copulations were very distinctive. Typically a male attempting an EPC would fly rapidly from elsewhere in the colony onto the back of a female on her nest and immediately begin treading. The female would either begin vocalizing loudly and struggling, or simply lift her tail and allow the male to copulate. After completing an EPC or EPC attempt, the male would return to his own nest area. In this study, all EPC attempts occurred when the pair male was absent from the nest site. Most females involved in EPCs were mounted by several males over several days. Only EPCs that occurred within a female's 'fertile' period (day -4 to day 1 after egg-laying) are considered in subsequent analyses. We did not observe EPCs prior to 4 days before egg-laying, although EPC attempts were observed during early incubation.

Feeding and parental care

Hatching occurred 23-25 days after incubation was initiated. We calculated feeding rates from approximately 5 days after hatching onwards, since at this point chicks obtain food directly from their parent's bill (Ploger & Mock, 1986). Earlier feeding rates were not considered reliable because parents regurgitate food directly into the nest, and often re-eat much of it later, confounding estimates of parental feeding effort. During later feeding, 2 chicks often grabbed the parent's bill simultaneously. The chick who had the uppermost position, and who was observed chewing or swallowing after the bolus was regurgitated, was considered successful.

Reproductive success

We considered any chick surviving to 35 days to have successfully fledged. In this study chicks did not leave the nest area until fledging, probably because neighbouring pairs, especially those in the early stages of breeding, were extremely aggressive to intruders near the nest and were observed to kill displaced chicks. We measured fledging success as the number of chicks fledged for all nests that successfully hatched chicks. Breeding success was measured as the number of chicks fledged for all pairs that laid eggs.

Behavioural sampling

We carried out two sets of intensive focal watches: (i) watches on pairing and parental care on 67 individual pairs between September 1989 and May 1990, and (ii) intensive copulation watches on 36 additional focal pairs between May and July 1990. For pairing and parental care watches we selected new pairs at three times: September 19 - October 14, $N = 13$; January 30 to March 15, $N = 34$; and May 21-30, $N = 20$. Pairs for intensive copulation

watches were chosen from June 1 to July 8, $N = 36$. If a selected pair failed or abandoned the site during nestbuilding or early incubation a new pair was chosen. Focal watches were conducted by two to four observers at any time.

For pairing and parental care watches, we observed pairs in the mornings (07:00-12:00) and afternoons (12:00-18:00) on alternate days. We increased sampling intensity during the January-April watches and observed pairs over all daylight hours (10 hours/day), except for a two-hr break taken at mid-day when activity levels were lowest. Since changes at the nest and feeding visits were infrequent, each observer was able to watch up to four pairs at a time.

We initiated focal watches the day after pairing, since cattle egrets attend their nest sites almost continuously after pairing and begin nestbuilding the day after pairing. Clutch size in Barbados varied from 1 to 3 eggs, with 2-egg clutches most common. We continued to observe pairs for 4-5 days after the first egg was laid, to ensure that we covered the entire fertile period. All nests were checked regularly during incubation, but focal watches were not conducted. Once hatch-243()TJ10013821639Tmm(tc)-27(h-243()013821631639Tmm(tc)-27(h-243T

over the study (range = 16-135 nests/survey, Krebs, 1991). Since cattle egrets interfere in conspecific breeding attempts by stealing nesting material and displacing and killing chicks, changes in the density of breeding birds in the colony could strongly influence pair behaviour. To control for this potential confounding factor, we initially included a measure of breeding density in all models.

± SE are reported throughout.
SPSS 10.0 (SPSS for Macintosh) was used for all analyses.

Results

Plumage and pairing patterns

The plumage scores of the male and female egrets sampled varied from 1 to 12 (males = 8.7 ± 0.3 , females = 5.5 ± 0.3 , $N = 135$ pairs). Plumage scores of breeding males and females varied over the year (Fig. 1). In particular, plumage scores were lower during February (Plumage scores by month — Males, $F_{7,127} = 65.8$, $p < 0.001$; Females, $F_{7,127} = 26.73$, $p < 0.001$; Fig. 1).

Male and female plumage scores were positively correlated within breeding pairs although male scores were higher in 79% of pairs (Pearson's correlation $r_p = 0.70$, $p < 0.001$; paired t -test = 13.7, $p < 0.001$; $N = 135$; Fig. 2). Females with high plumage scores did not pair with males with low scores, but

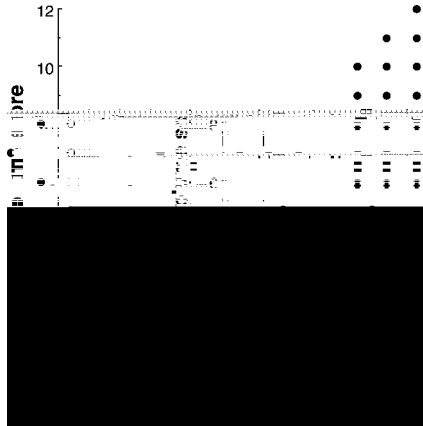
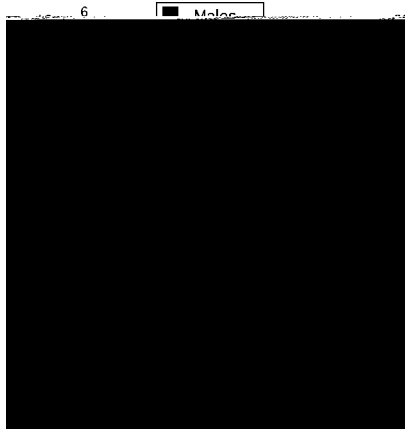


TABLE 2. Variables affecting breeding behaviour and parental care

Response variables	Colony density			Male plumes		Female plumes	
	<i>N</i>	<i>F</i>	<i>p</i> value	<i>F</i>	<i>p</i> value	<i>F</i>	<i>p</i> value
Male nest attendance	45	1.21	0.28	0.05	0.83	4.05	0.05
Female nest attendance	45	0.01	0.92	1.78	0.19	0.55	0.46
Female alone at nest	45	0.59	0.45	0.32	0.57	4.22	0.05
Pair copulation rate	52	0.44	0.51	19.92	<0.001	6.39	0.01
Male nesting attendance	23	1.93	0.19	0.00	0.98	2.56	0.13
Female nestling attendance	23	0.38	0.55	2.4	0.14	0.37	0.55
Male feeding rate/chick	23	0.47	0.50	8.03	0.01	1.12	0.30
Female feeding rate/chick	23	0.20	0.66	1.09	0.31	1.48	0.24
Male feeding proportion	23	0.42	0.53	1.33	0.26	0.07	0.79

Summary of GLM models examining the influence of (i) breeding density (number of nests) at the colony, (ii) male plume score and (iii) female plume score on the breeding behaviour and parental care of pairs of cattle egrets (see Methods for a description of each variable). Breeding density was dropped from the final model in all cases because it was non-significant. Final models retain both male and female plume scores in order to control for the influence of a mate's plumes. Sample sizes vary due to mortality at different stages and are reported under each variable. All significant results are presented in bold.

Nest and mate guarding

Nest attendance was unrelated to breeding density in the colony (Table 2). Overall, males spent more time at the nest site than females in the pre-egg-laying period (proportion of observations in attendance, males = 0.72 ± 0.02 , females = 0.53 ± 0.02 ; paired *t*-test = 5.25, *df* = 44, *p* < 0.001). Although nest sites were not continuously attended, male and

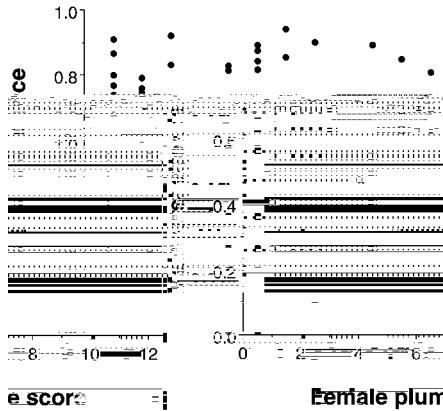


Fig. 3. Male nest attendance (proportion of time at nest) during the pre-egg-laying phase plotted against female plume scores for each pair ($N = 45$).

Copulation patterns

Cattle egret pairs ($N = 52$) copulated 0.086 ± 0.008 times/hr over the fertile period. Rates were unrelated to the density of pairs breeding in the colony (Table 2). Controlling for female plumage, well-plumed males had higher in-pair copulation rates than more poorly plumed males ($F_{1,49} = 19$).

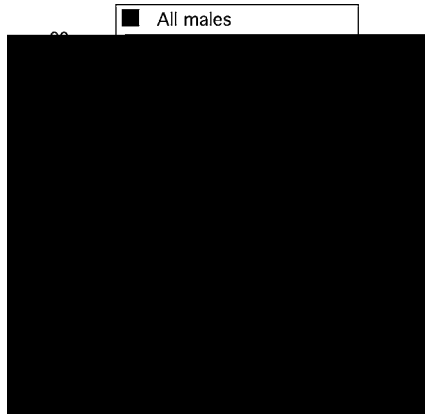


Fig. 4. The distribution of plume scores for all males sampled ($N = 46$), and males who were observed engaging in EPCs ($N = 22$).

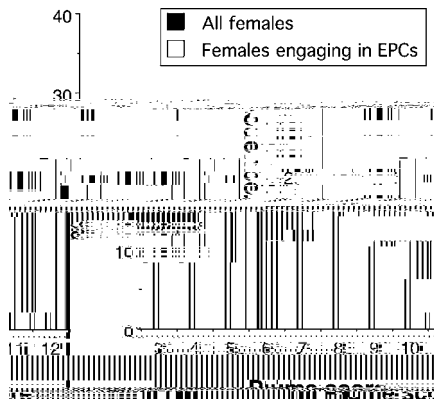


Fig. 5. The distribution of plume scores for the females that were not observed to engage in EPCs ($N = 59$) and for females that were observed to engage in EPCs ($N = 22$).

$= 0.08$, $p = 0.77$), but they were more likely to engage in EPCs when extra-pair males had better plumes than those of their mate (paired t -test; $t_{12} = 2.89$, $p = 0.01$).

Care of nestlings

Males and females attended nestlings at similar rates (Proportion of observations in attendance: males = 0.32 ± 0.03 , females = 0.33 ± 0.03 , $t_{22} = 0.18$,

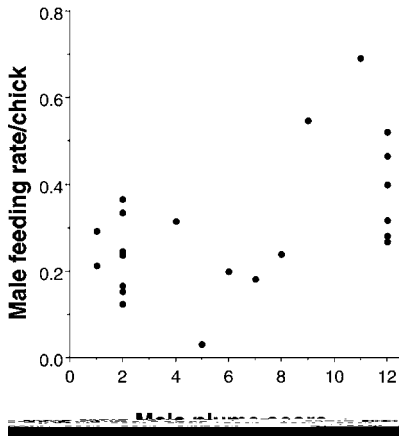


Fig. 6. Male feeding rate (bolu001256nET0.13m4CET86EIRhru001/6Tm[ra]-27(te)-714CET86EIP

have lower plume scores than those who did not (edged chicks: 2.8 ± 0.6 , $N = 42$, edged none: 3.9 ± 0.5 , $N = 22$; Logistic regression controlling for male plumes — Wald $\chi_1^2 = 3.76$, $p = 0.053$). Fledging success was unrelated to nesting density in the colony (Wald $\chi_1^2 = 0.15$, $p = 0.70$).

Since cattle egret nests can be destroyed in their early stages by conspecifics, and early parental vigilance is therefore likely to be important, we examined whether the breeding success of birds observed from pairing was predicted by their plume scores. Overall, pairs produced 0.73 ± 0.09 chicks per breeding attempt. The plumes of neither males nor females were scored higher for successful pairs (Males: edged chicks = 6.7 ± 0.7 , $N = 30$, edged none = 6.6 ± 1.0 , $N = 30$; Logistic regression controlling for female plumes — Wald $\chi_1^2 = 0.84$, $p = 0.36$; Females: edged chicks = 3.5 ± 0.5 , $N = 30$, edged none = 4.4 ± 0.6 , $N = 30$; Logistic regression controlling for male plumes — Wald $\chi_1^2 = 2.02$, $p = 0.16$). Breeding success was not influenced by nesting density in the colony (Wald $\chi_1^2 = 0.56$, $p = 0.45$).

Discussion

Like many monogamous species in the heron family, both male and female cattle egrets develop conspicuous plumes in the breeding season (Hancock & Kushlan, 1984). These lamentous breeding plumes are used primarily in courtship and are absent in the non-breeding season, supporting Darwin's (1871) suggestion that the ornamental plumage found in herons is a sexually selected character. We found that male cattle egrets were, on average, more ornamented than females although both sexes developed breeding plumes that spanned the range of our scoring system. Female cattle egrets appeared to have stronger pairing preferences than males and rarely paired with males less well-plumed than themselves. Breeding plumes were correlated primarily with the behaviour of males, suggesting that females obtain material benefits from pairing with well-plumed mates. However, females also selectively accepted EPCs from better plumed males, suggesting that plumes may also signal genetic benefits.

Female mating preferences

Female cattle egrets observe displaying males in the colony before pairing, suggesting that they actively choose mates based on breeding plumes. How-

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