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

by

ELIZABETH A. KREBS[1,2,3], **WAYNE HUNTE**[1] **and DAVID J. GREEN**[1,4]
([1] Department of Biology, McGill University, Montreal, P.Q., H3A 1B1, Canada and Bellairs Research Institute of McGill University, St. James, Barbados, West Indies; [2] Centre for Wildlife Ecology, Department of Biological Sciences, Simon Fraser University, Burnaby, BC, V5A 1S6, Canada)

(Acc. 6-II-2004)

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

---

[3] Author for correspondence: Elizabeth Krebs, Centre for Wildlife Ecology, Department of Biological Sciences, Simon Fraser University, Burnaby, BC, V5A 1S6, Canada, e-mail: ekrebs@sfu.ca

[4] We thank Janet Dickie, Stephane Perrault, Zena Tooze and the Bellairs crew for invaluable help and lively discussion in the field. Dave Putland kindly wrote and ran the randomisation program. Thanks to Doug Mock and an anonymous reviewer for insightful comments from a Cenozoic perspective. This research was supported by NSERC grant AO264 to WH and a NSERC postgraduate scholarship to EAK. The refurbishment of this manuscript was made possible by a University of Queensland Postdoctoral Fellowship to EAK and an Ecology Centre Postdoctoral Fellowship to DG.

Behaviour 141, 479-499

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 pair with males with more conspicuous plumage characteristics (Burley, 1986; Møller, 1988; Norris, 1990a; Hill, 1991) and/or engage in extra-pair copulations ('EPCs') with more colorful or elaborately plumed males (*e.g.* Møller, 1988, 1997; Yezerinac & Weatherhead, 1997, but see Hill *et al.*, 1994, for an example of opposing pairing and EPC preferences). Intra-sexual variation in mate quality in monogamous species can lead to differing mating preferences expressed by both males and females (Trivers, 1972; Burley 1986; see Johnson, 1988a, b). For example in barn owls (*Tyto alba*) males choose females based on the spottiness of their plumage but females choose males based on plumage coloration (Roulin, 1999; Roulin *et al.*, 2001).

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 Ardeids are displayed extensively during courtship (Mock, 1976, 1978), suggesting that they play a role in mate choice. We assessed the function of breeding plumes by examining how variation in breeding plumes was associated with (i) pairing patterns (ii) the quality of parental care, and (iii) the distribution of extra-pair copulations.

Methods

We observed breeding pairs of cattle egrets nesting in part of a colony (*ca* 1000 birds) situated in North-east Barbados between September 1989 and July 1990 (see Krebs, 1991, for number and location of cattle egret colonies in Barbados). Cattle egrets in Barbados breed throughout the year, with varying peaks of activity (Riven-Ramsey, 1988; Krebs, 1991). Prior to breeding, both sexes develop reddish-brown filamentous plumes on the head, back and chest (Blaker, 1969). Immediately prior to pairing cattle egrets also acquire a distinctive red coloration in the legs, bill, lores and irises (Blaker, 1969). Thus, unpaired birds that are ready to breed and newly paired birds were easily identified throughout the study period.

To track the seasonal breeding phenology, we estimated colony density by weekly counts of all visible nesting pairs, categorized by breeding stage, from a fixed distance from the colony (Krebs, 1991). We followed the breeding behaviour of pairs by monitoring individual 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 of the nest. Since watches and nest checks occurred every day, we were able to precisely determine the timing of any breeding failures.

Breeding plumes

Since ambient light, wind conditions and behaviour (plumes are fluffed when displaying) can influence the appearance of plumes, we chose to rate the extent of plume development in categories that could be easily assessed by observers. Plumage scores were assigned to birds at the start of a breeding attempt, when new breeding birds were distinctive because of their red legs, bills and lores. We assessed the length of plumes on the head, back and chest of each bird visually and assigned plume scores as described in Table 1. Head plumes were scored based on the distance they extended over the head, and on their density: sparse (few filaments, intermittent and wispy appearance), or lush (many filaments, dense brush-like appearance). Plumes on the chest and back area were scored based on their length relative to the bird's body, and their colour: dark (red-brown) or pale (light orange to white). Higher plume scores reflect increasing length, colour and density of plumes. Plume scores were evaluated at least twice during the first week and were reassessed during chick rearing; in no case did an individual's breeding plume score change over a breeding attempt. To ensure consistency, all scores were verified by one observer approximately one week after observations commenced (EAK). To minimize any variation in assigning plumage scores we have used very broad categories (*e.g.* $<1/3$ length of chest *vs* $>1/3$; see Table 1).

Plume scores on an individual's head, chest and back were intercorrelated for both males and females (*i.e.* head with chest, head with back, chest with back; Spearman's rank correlation; $r_s > 0.73$ for males and $r_s > 0.72$ for females). To maximize the variation in individual plume scores we have summed the plume scores from each body part to give a total plume score (range 0-12) for each individual (rather than 0-4 for each part), and only total plume scores are used in subsequent analyses.

Sex determination

The sex of each bird was determined behaviourally using sex specific behaviours such as male courtship, nest site acquisition, and twig collecting as cues (see Blaker, 1969, for a description). Copulation position was subsequently used to confirm our assigned sex. Only one pair had to be discarded because of inconsistencies between courtship behaviour and copulation position. This pair engaged in frequent 'reverse' copulations and subsequently failed to lay eggs. Thus, although our sexes were not confirmed by genetic analysis, we believe our behavioural assignments were, for all but one pair, consistent and clear. Once sex had been determined, differences in plume development and/or idiosyncrasies of the face or plumes were used to continue differentiating the pair. We were able to do this with a high degree of accuracy because we observed birds daily for relatively long periods, so that any changes in nesting pairs in the neighbourhood were quickly detected. In our sample, only two birds were ever associated with a given nest site and the plume scores of individuals never changed in such a way as to suggest sudden mate switching.

TABLE 1. *Scoring system used to assign plume scores to breeding plumes on the head, chest and back of individual cattle egrets (see Methods for details)*

Area	Score	Description
Head	0	no plumes
	1	sparse plumes in front of head only
	2	sparse plumes extending down back of head
	3	lush plumes in front of head
	4	lush plumes extending down back of head
Chest	0	no plumes
	1	<1/3 length of chest, pale in colour
	2	<1/3 length of chest, dark in colour
	3	>1/3 length of chest, pale in colour
	4	>1/3 length of chest, dark in colour
Back	0	no plumes
	1	<1/2 length of back, pale or dark
	2	>1/2 length of back, pale or dark
	3	>3/4 length of back, pale in colour
	4	>3/4 length of back, dark in colour

Courtship and pairing

An unpaired red-billed male cattle egret acquires and defends a small display territory in the colony from both male and female intruders. Courtship displays are performed, primarily during early morning and late afternoon, for up to 1 week, although some males pair on their first afternoon of displaying. Females exhibit more evident mate choice than males. They move through the colony and watch males display. We have seen up to six females simultaneously watching a nearby displaying male. Pairing is initiated by females, who attempt to land on the back of a displaying male (submission mount, Blaker, 1969). The male appears to resist the advances of a female, and often displaces her. A female may mount the same male many times before pairing with him. Two birds were considered to have paired when mutual backbiting was observed (Blaker, 1969; Krebs, 1991).

Within-pair and extra-pair copulation patterns

Copulation in cattle egrets is believed to occur at or near the nest site (Fujioka & Yamagishi, 1981; McKilligan, 1990), and indeed, all copulations observed in this study occurred within 1 m of the nest. Copulations were recorded opportunistically during behavioural observations. All copulations were recorded as either intra-pair or extra-pair, and the plumage and, if known, the identity of the male and female involved was noted. Copulations were termed 'successful' if the female was observed to lift her tail, and/or the male performed lateral wipes. Unsuccessful copulations fell into two categories. If the female struggled, vocalized and attempted to displace the male, copulations were termed 'resisted'; such copulations appeared not to result in sperm transfer since males did not appear to be able to achieve 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 egglaying) are considered in subsequent analyses. We did not observe EPCs prior to 4 days before egglaying, 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 free flying, 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 hatching had occurred we observed nests until the chicks were free-flying at 35-45 days old. The maximum observation period for any one pair was 79 days. During focal watches we recorded the behaviour of each pair member every minute and opportunistically recorded all discrete behaviours such as copulations and aggressive interactions, as well as the number of boluses delivered to each chick by either parent. Pairing and parental care watches on nests ($N = 67$) totaled 7699.5 nest-hrs of observation over the whole study.

For intensive copulation watches we observed pairs from sunrise until noon or from noon until dusk, on alternate days. Each focal pair was observed from pairing until four days after clutch initiation (7-13 days of observation). To evaluate the variation in breeding plumes in the colony during these watches, in addition to the focal pairs, we assessed the breeding plumes of any other newly breeding pairs in the same subsection of the colony ($N = 32$). During focal watches we recorded the presence or absence at the nest of each pair member each minute, and scanned continuously for copulations, aggressive interactions and nestbuilding activities. Intensive copulation watches were conducted on 36 nests for a total of 973.0 nest-hrs.

Variable definition and statistical analysis

Discrete behaviours are reported as rates (# observed/hr). Attendance was calculated as the proportion of time spent at the nest per day.

Chicks were attended constantly by parents for a period ranging from 8 to 19 days after hatching. To compare the intensity of chick attendance during the nestling period, we calculated parental attendance rates from 9 to 21 days after hatching, only for those pairs who successfully fledged chicks. All parental attendance of chicks, except feedings, ceased by 21 days posthatch.

Total chick-feeding rates declined from 5 to 40 days after hatching ($r_S = -0.55$, $p < 0.001$, $N = 103$). Since this may reflect changes in bolus sizes that we were unable to monitor, only birds that were monitored over the whole nestling phase were used in feeding rate analyses. To control for any variation associated with diurnal changes and infrequent feeding visits (*ca* 1/hr), we calculated an overall feeding rate (boluses delivered/chick/hr) for all observation periods. The parents' relative feeding effort was also assessed as the proportion of the total boluses that were brought to the nest by the male.

We used GLM models to examine whether breeding plumage influences breeding performance in cattle egrets. The density of breeding birds in the colony varied considerably 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. Nine different aspects of breeding and parental behaviour were tested as response variables: (i, ii) male and female nest attendance prior to egglaying (# min at nest/total min observed), (iii) proportion of time a female was alone at the nest during the fertile period (# min alone/total min observed), (iv) copulation rates (# observed/hr) (v, vi) male and female nestling attendance (# min with chicks/total min observed), (vii, viii) male and female feeding rates (# boluses/chick/hr), and (ix) proportion of boluses delivered by the male. We tested each response variable against the following explanatory variables: male plume scores, female plume scores and a measure of breeding density at the colony over the time the response variable was measured (*e.g.* colony density during the nestling period). We tested for interactions between plume scores and colony density, but since no interactions were significant ($p > 0.20$ in all cases) we do not report them. To compare rates of male and female behaviours within a pair we used paired t-tests and Pearson's correlation coefficients.

Cattle egrets fledged one and rarely two young, so for analyses of fledging and breeding success we categorized pairs as either successful or unsuccessful. We used multiple logistic regression on these binary variables to assess the effects of male and female plume scores.

We assessed whether males that engaged in EPCs were a random subset of the population using a resampling procedure (Resampling Stats, http://www.resample.com/). In this analysis we randomly sampled 22 males from the distribution of plume scores in the colony during copulation watches 10,000 times and determined the probability that the observed plume distribution of 22 known extra-pair males would be obtained. We evaluated whether male or female plume scores influenced whether a female cuckolded her mate using logistic regression.

We tested whether models conformed to the assumptions of normality and equal variances by examining residual and normal probability plots. Mean ± SE are reported throughout. SPSS 10.0 (SPSS for Macintosh) was used for all analyses.

Results

Plumage and pairing patterns

The plume scores of the male and female egrets sampled varied from 1 to 12 (males $= 8.7 \pm 0.3$, females $= 5.5 \pm 0.3$, $N = 135$ pairs). Plume scores of breeding males and females varied over the year (Fig. 1). In particular, plume scores were lower during February (Plume 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 plume 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 plume scores did not pair with males with low scores, but

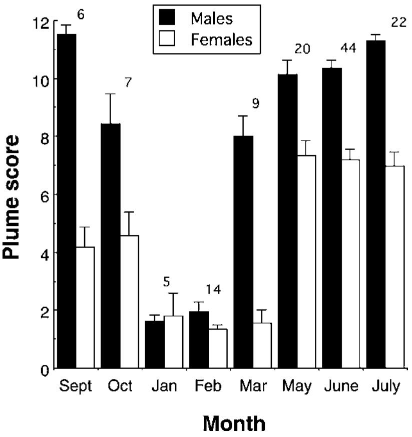

Fig. 1. Plume scores for pairs initiating breeding in each month across the study (mean ± SE). Male scores (black bars) and female scores (white bars) are presented separately. The number of pairs sampled is indicated over each set of bars. Note that no birds were sampled during November, December or April.

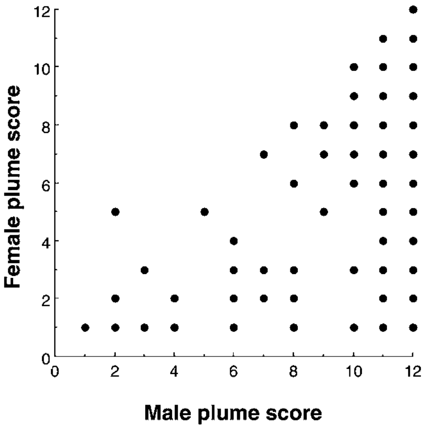

Fig. 2. Female plume scores plotted against the male partner's plume score for all breeding pairs sampled ($N = 135$). Some points represent more than one breeding pair.

males with high scores paired with females whose plumage varied considerably (Fig. 2). Nevertheless, males who re-paired during nest-building did so with better plumed females than their original mates (paired t-test $= 3.74$, df $= 7$, $p < 0.01$) suggesting some preference by males for better plumed females.

TABLE 2. *Variables affecting breeding behaviour and parental care*

Response variables		Colony density		Male plumes		Female plumes	
	N	*F*	*p* value	*F*	*p* value	*F*	*p* 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-egglaying period (proportion of observations in attendance, males $= 0.72 \pm 0.02$, females $= 0.53 \pm 0.02$; paired t-test $= 5.25$, df $= 44$, $p < 0.001$). Although nest sites were not continuously attended, male and female attendance at the nest were negatively correlated ($r_{\mathrm{p}} = -0.51$, $p < 0.001$, $N = 45$).

Male nest attendance was positively correlated with plume score of their mate, but not with the males' own plume score (Table 2, Fig. 3). In contrast female nest attendance was not correlated with their own plume score or that of their mate (Table 2).

Since the pre-egglaying period encompasses the female's fertile period, one function of male attendance may be mate guarding. Time that a female spent unattended at the nest site in the pre-laying period was negatively correlated with female, but not male plume scores (Table 2).

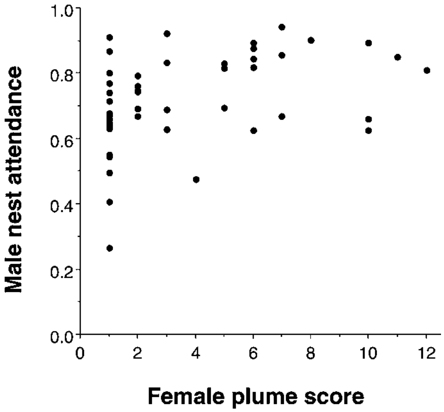

Fig. 3. Male nest attendance (proportion of time at nest) during the pre-egglaying phase plotted against female plume scores for each pair ($N = 45$).

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 ($F_{1,49} = 19.9$, $p < 0.001$); similarly, controlling for male plumage, in-pair copulation rates were higher for well plumed than for poorly plumed females ($F_{1,49} = 6.4$, $p = 0.01$).

Ten percent (30/295) of all copulations observed at the colony were EPCs. Our estimates of EPC rates were higher for the intensively observed focal pairs (15.5%, 24/155) than for other pairs in the study (4%, 6/140; see Methods); this is unsurprising given the rapid and surreptitious nature of EPCs. To reduce the effects of biases in detectability, we have restricted subsequent analyses to the data collected during intensive copulation watches (see Methods for details).

Only males with plume scores greater than 10 were observed engaging in EPCs, and EPC males were better plumed than other males in the colony at the time (p that all EPC males would have plume scores >10 by chance $=$ 0.01; Fig. 4). However males who were successful at EPCs did not differ in plume scores from those of males who were not ($t_{21} = 0.03$, $p = 0.98$).

Well plumed females also tended to be more likely to engage in EPCs than poorly plumed females (Wald $\chi^2_1 = 3.21$, $p = 0.07$; Fig. 5). Females were

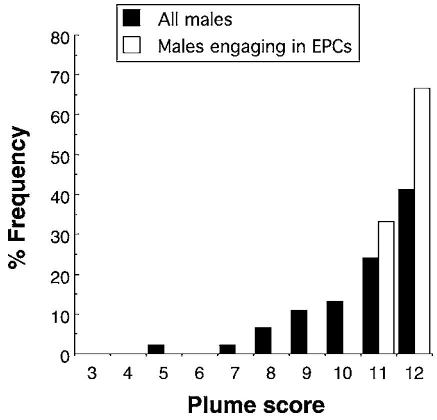

Fig. 4. The distribution of plume scores for all males sampled ($N = 46$), and males who were observed engaging in EPCs ($N = 22$).

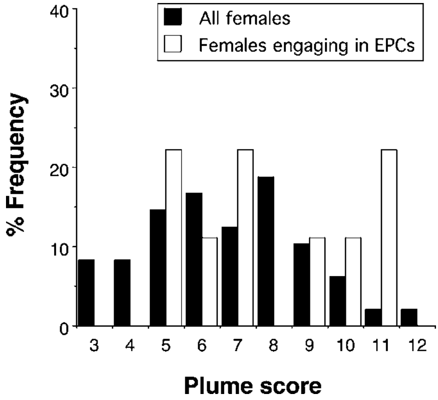

Fig. 5. The distribution of plume scores for the females that were not observed to engage in EPCs ($N = 59$) and for females that were observed to engage in EPCs ($N = 9$).

not more likely to cuckold a mate who had poor plumes (Wald $\chi^2_1 = 0.08$, $p = 0.77$), 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 $= 0.32 \pm 0.03$, females $= 0.33 \pm 0.03$, $t_{22} = 0.18$,

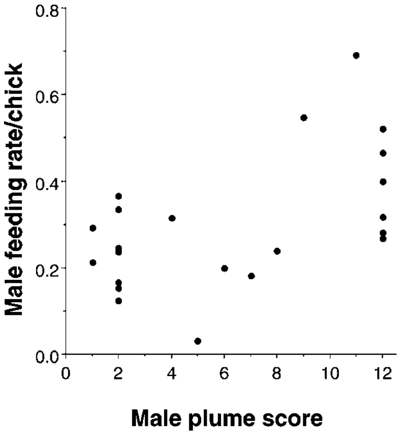

Fig. 6. Male feeding rate (boluses/hr/ chick) during the nestling period plotted against male plume scores for all pair who successfully fledged chicks ($N = 23$).

$p = 0.86$), and attendance by the members of a pair was positively but not significantly correlated ($r_p = 0.30$, $p < 0.15$, $N = 23$). Neither male nor female nestling attendance was correlated with male or female plume scores within pairs (Table 2). Parental attendance was not related to the density of nests in the colony during the nestling phase (Table 2).

Overall chicks were fed 0.59±0.05 boluses/chick/hr ($N = 23$). Males and females fed at similar rates (males = 0.30 ± 0.03 boluses/chick/hr, females = 0.33 ± 0.03; $t = 0.19$, $p = 0.85$). Neither male nor female feeding rates were related to the density of nests at the colony (Table 2).

Well plumed males fed chicks at higher rates than poorly plumed males (Table 2, Figure 6), but males with well plumed mates did not feed at higher rates than other males (Table 2). Female feeding rate was correlated with neither her own nor her mate's plume scores (Table 2).

Reproductive success

We found no evidence that fledging success of well plumed birds was higher than that of poorly plumed birds. In this study, pairs fledged an average of 0.92 ± 0.09 chicks. Among pairs that hatched at least one egg, males who fledged chicks did not have higher plume scores than males who did not (fledged chicks: 6.3±0.7, $N = 42$; fledged none: 6.2±1.0, $N = 22$; Logistic regression controlling for female plumes — Wald $\chi^2_1 = 1.94$, $p = 0.16$). Contrary to expectation, females who successfully fledged chicks tended to have lower plume scores than those who did not (fledged chicks: 2.8 ± 0.6, $N = 42$, fledged 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: fledged chicks $= 6.7 \pm 0.7$, $N = 30$, fledged none $= 6.6 \pm 1.0$, $N = 30$; Logistic regression controlling for female plumes — Wald $\chi_1^2 = 0.84$, $p = 0.36$; Females: fledged chicks $= 3.5 \pm 0.5$, $N = 30$, fledged none $= 4.4 \pm 0.6$, $N = 30$; 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 filamentous 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. However, the patterns of assortative mating we observed are consistent either with female mating preferences or intra-sexual competition restricting female mate choice (Burley, 1983). We do not know if well plumed females are competitively superior, but we did observe up to six females watching and even fighting over a single displaying male, suggesting that competition over males can occur.

Female cattle egrets also appear to prefer well plumed males as extra-pair partners. Extra-pair copulations are unlikely to occur because of coercion by males; like Fujioka & Yamagishi (1981) and McKilligan (1990), we observed female cattle egrets resisting or refusing extra pair copulations and we infer that females are able to selectively engage in EPCs.

Pairing with a better plumed male provides female cattle egrets with at least two potential direct benefits. Females obtained higher levels of parental care from more ornamented males, a pattern that has been observed in a few other species (Norris, 1990b; Voltura *et al.*, 2002; Daunt *et al.*, 2003). Theoretical models show that elaborate breeding plumage can evolve to signal direct benefits via a fecundity advantage accrued through male parental care (Hoelzer, 1989; Heywood, 1989; Price *et al.*, 1993). Females cattle egrets paired to well plumed males may also benefit through higher fertility as a result of higher copulation rates, but if well plumed males have higher fertility, females paired to poorly plumed males should seek out EPCs as 'fertility insurance' (Sheldon, 1994; Petrie & Kempenars, 1998). Our data do not support this hypothesis, since females with poorly plumed mates were not especially likely to engage in EPCs, nor were EPCs especially common when male breeding plumes were most poorly developed in the colony; 10% of all EPCs were observed when plume scores were low.

Our data suggest that cattle egret plumes signal more than direct benefits. Females potentially obtain genetic benefits, via increased viability or attractiveness of their offspring, when they pair or engage in EPCs with well plumed mates. Although we have no data on the survival of well plumed individuals, sexually selected traits are associated with viability in other species (*e.g.* Norris, 1993; Petrie, 1994). In socially monogamous species, variation in EPC success is likely to be the major source of variance in mating success between males, so females may obtain indirect benefits by pairing with males bearing traits that make them more successful at EPCs (Hamilton, 1990). However, a preference for ornamental traits in extra-pair mates has been described in only a few species (swallows *Hirundo rustica*, Møller, 1988; zebra finches *Poephila guttata*, Houtman, 1991); few studies have identified traits associated with EPC success, but the most common such trait is age (*e.g.* Morton *et al.*, 1990; Westneat, 1990; Wetton *et al.*, 1995; Perrault *et al.*, 1997; Richardson & Burke, 1999).

Male mating preferences

The patterns of pairing observed in this study suggest that male cattle egrets were less selective than females in choosing a mate. However, males were not unselective: males only re-paired with females that had more developed plumes than their original mates. Male mate choice may have been constrained either by male-male competition or through a male sex ratio bias at the colony. Although the extent of plume development varied seasonally, we observed males of widely varying breeding plumage displaying close to each other, suggesting that access to nesting sites was not determined by plume development. The sex ratio at colonies can vary seasonally in other Ardeids (*e.g.* little egrets *Egretta garzetta*; Fujioka, 1989). In our study not all displaying males appeared to pair, suggesting the colony sex ratio could be male-biased.

The primary reason for males to be less discriminating than females at pairing is because pairing does not preclude males from attempting to increase their mating success in other ways, such as through EPCs (Johnstone *et al.*, 1996). EPCs are frequent in cattle egrets and other colonial Ardeids (Fujioka & Yamagishi, 1981; McKilligan, 1990; this study), and in colonial species, pairing and defending a nesting site may actually increase male extra-pair mating success by allowing males to monitor the fertility of nearby females (Magrath & Elgar, 1997). Consistent with this theory, most EPCs in cattle egrets have been observed between neighbouring pairs (McKilligan, 1990; this study).

Pairing with a well plumed female provided no measured immediate benefit to males. No aspect of parental care was correlated with female plumage score, but males appeared to invest more when paired to well plumed females by increasing nest attendance, mate guarding and copulations. High rates of mate guarding and copulation both function as paternity assurance mechanisms (Lovellmansbridge & Birkhead, 1998; Komdeur *et al.*, 1999), while nest attendance will reduce nesting failure through conspecific theft of nest material, which can be high in Ardeids (Frederick, 1987; McKilligan; 1990). The fact that males appeared to increase their investment when breeding with a well-plumed female suggests that these females were of higher genetic quality. (Well-plumed females were not sought out by males as extra-pair partners, but the low costs of engaging in EPCs may lead to little discrimination by males; Petrie & Kempenaers, 1998.) If well-plumed females are of higher genetic quality, then their offspring should have more elaborate plumes, or higher viability. Well-plumed females were not more likely to fledge young than poorly plumed females, although our ability to discriminate between the reproductive success of pairs was limited by the small clutch sizes in Barbados and a lack of information on the quality or survival of young produced.

Mutual mate choice

In monogamous species both the benefits and costs of mate choice should be similar for the two sexes, leading to a potential for mutual mate choice. Johnstone *et al.* (1996) predict that mutual mate choice should be especially likely in colonial species because the large number of potential mates reduces the costs of mate rejection. The extent of mutual mate choice across species is unclear, but it has been demonstrated in a few species, including pinyon jays *Gymnorhinus cyanocephalus* (Johnson, 1988a, b), crested auklets *Aethia cristatella* (Jones & Hunter, 1993, 1999) and barn owls *Tyto alba* (Roulin, 1999; Roulin *et al.*, 2001).

We found that in cattle egrets a single ornamental trait may be correlated with both parental ability and some aspect of genetic quality. One type of trait that could signal both viability and parental ability is an age-dependent trait (Manning, 1987, 1989). Plumage colour, elaboration and overall development are correlated with male age in many species (*e.g.* peacocks, Petrie *et al.*, 1991; Galapagos finches *Geospiza conirostris*, Grant & Grant, 1987; long-tailed skuas *Stercorarius longicaudus*, Andersson, 1976, 1994; satin bowerbirds Collis & Borgia, 1993) and parental age and experience are also frequent correlates of breeding success (*e.g.* Daunt *et al.*, 1999; Espie *et al.*, 2000; see Saether, 1990, for a review). In cattle egrets, at least some of the variability in plume development is likely to be age-related since Maddock (1989) noted increased plume development between banded first and second year birds in the Australian subspecies of cattle egret (*B. ibis coromandus*). Plume development may also be condition-dependent in cattle egrets since the colour is carotenoid-based and must be acquired from the diet (Fox, 1976). Plumage colour honestly signals male condition and genetic quality in house finches (*Carpodacus mexicanus*), in which brightly coloured males fed young at a higher rate, survived better and were preferred by females (Hill, 1991). If plumes honestly signal age and condition in cattle egrets, a preference for well plumed mates may select for both better parental care and genetic quality.

Few studies have tested whether both sexes discriminate among potential mates on the basis of ornamental traits, despite the fact that many monomorphic species have conspicuous ornaments (Jones & Hunter, 1999; see Amundsen, 2000, for a review). In this study, mate choice for breeding plumes appeared to provide direct fitness benefits to females and indirect fitness benefits to both sexes. The breeding plumages seen in both sexes of many Ardeids would make them a model system for future work on the development of ornaments and benefits of mutual mate choice.

References

Amundsen, T. (2000). Why are female birds ornamented? — Trends Ecol. Evol. 15, p. 149-155.

Andersson, M. (1976). Population ecology of the long-tailed skua (*Stercorarius longicaudus* Vieill.). — J. Anim. Ecol. 45, p. 537-559.

— — (1994). Sexual selection. — Princeton University Press, Princeton.

Blaker, D. (1969). Behaviour of the cattle egret *Ardeola ibis*. — Ostrich 40, p. 75-129.

Borgia, G. (1985). Bower quality, number of decorations and mating success of male satin bowerbirds (*Ptilonorhynchus violaceus*) — an experimental analysis. — Anim. Behav. 33, p. 266-271.

Burley, N. (1983). The meaning of assortative mating. — Ethol. Sociobiol. 4, p. 191-203.

— — (1986). Sexual selection for aesthetic traits in species with biparental care. — Am. Nat. 127, p. 415-445.

Collis, K. & Borgia, G. (1993). The costs of male display and delayed plumage maturation in the satin bowerbird (*Ptilonorhynchus violaceus*). — Ethology 94, p. 59-71.

Darwin, C. (1871). The descent of man and selection in relation to sex. — Murray, London.

Daunt, F., Wanless, S., Harris, M.P. & Monaghan, P. (1999). Experimental evidence that age-specific reproductive success is independent of environmental effects. — Proc. Roy. Soc. London B 266, p. 1489-1493.

— —, Monaghan, P., Wanless, S. & Harris, M.P. (2003). Sexual ornament size and breeding performance in female and male European shags *Phalacrocorax aristotelis*. —- Ibis 145, p. 54-60.

Espie, R.H.M., Oliphant, L.W., James, P.C., Warkentin, I.G. & Lieske, D.J. (2000). Age-dependent breeding performance in merlins (*Falco columbarius*). — Ecology 81, p. 3404-3415.

Frederick, P. 1987. Extra-pair copulations in the mating system of white ibis (*Eudocimus albus*). — Behaviour 100, p. 170-201.

Fisher, R.A. (1915). The evolution of sexual preference. — Eugenics Review 7, p. 184-192.

— — (1930). The genetical theory of natural selection. — Clarendon, Oxford.

Fox, D.L. (1976). Animal biochromes and structural colors. — University of California Press, Berkeley.

Fujioka, M. (1989). Mate and nestling desertion in colonial little egrets. — Auk 106, p. 292-302.

— — & Yamagishi, S. (1981). Extramarital and pair copulations in the cattle egret. — Auk 98, p. 134-144.

Grant, B.R. & Grant, P.R. (1987). Mate choice in Darwin's finches. — J. Linn. Soc. 32, p. 247-270.

Hamilton, W.D. (1990). Mate choice near or far? — Am. Zool. 30, p. 341-352.

Hancock, J. & Kushlan, J.A. (1984). The herons. — Croom Helm, London.

Heywood, J.S. (1989). Sexual selection by the handicap mechanism. — Evolution 43, p. 1387-1397.

Hill, G.E. (1991). Plumage coloration is a sexually selected indicator of male quality. — Nature 350, p. 337-339.

— —, Montgomerie, R., Roeder, C. & Boag, P. (1994). Sexual selection and cuckoldry in a monogamous songbird: implications for sexual selection theory. — Behav. Ecol. Sociobiol. 35, p. 193-199.

Hoelzer, G.A. (1989). The good parent process of sexual selection. — Anim. Behav. 38, p. 1067-1078.

Houtman, A.M. (1992). Female zebra finches choose extra-pair copulations with genetically attractive males. — Proc. Roy. Soc. London B 249, p. 3-6.

Johnson, K. (1988a). Sexual selection in pinyon jays I: female choice and male-male competition. — Anim. Behav. 36, p. 1038-1047.

— — (1988b). Sexual selection in pinyon jays II: male choice and female-female competition. — Anim. Behav. 36, p. 1048-1053.

Johnstone, R.A., Reynolds, J.D. & Deutsch, J.C. (1996). Mutual mate choice and sex differences in choosiness. — Evolution 50, p. 1382-1391.

Jones, I.L. & Hunter, F.M. (1993). Mutual sexual selection in a monogamous seabird. — Nature 362, p. 238-239.

— — & — — (1999). Experimental evidence for mutual inter- and intrasexual selection favouring a crested auklet ornament. — Anim. Behav. 57, p. 521-528.

Komdeur, J., Kraaijeveld-Smit, F., Kraaijeveld, K. & Edelaar, P. (1999). Explicit experimental evidence for the role of mate guarding in minimizing loss of paternity in the Seychelles warbler. — Proc. Roy. Soc. London B 266, p. 2075-2081.

Krebs, E.A. (1991). Reproduction in the cattle egret (*Bubulcus ibis ibis*): The function of breeding plumes. — M.Sc. Thesis, McGill University.

Lovellmansbridge, C. & Birkhead, T.R. (1998). Do female pigeons trade pair copulations for protection? — Anim. Behav. 56, p. 235-241.

Maddock, M. (1989). Colour and first age of breeding in cattle egrets as determined from wing-tagged birds. — Corella 13, p. 1-8.

Magrath, M.J.L. & Elgar, M.A. (1997). Paternal care declines with increased opportunity for extra-pair matings in fairy martins. — Proc. Roy. Soc. London B 264, p. 1731-1736.

Manning, J.T. (1985). Choosy females and correlates of male age. — J. theor. Biol. 116, p. 349-354.

— — (1989). Age-advertisement and the evolution of the peacock's train. — J. Evol. Biol. 2, p. 379-384.

McKilligan, N.G. (1990). Promiscuity in the cattle egret (*Bubulcus ibis*). — Auk 107, p. 334-341.

Mock, D.W. (1976). Pair-formation displays of the great blue heron. — Wilson Bull. 88, p. 184-230.

— — (1978). Pair-formation displays of the great egret. — Condor 80, p. 159-172.

Møller, A.P. (1988). Female choice selects for male sexual tail ornaments in the monogamous swallow. — Nature 332, p. 640-642.

— — (1997). Immune defence, extra-pair paternity, and sexual selection in birds. — Proc. Roy. Soc. London B 264, p. 561-566.

Morton, E.S., Forman, L. & Braun, M. (1990). Extra-pair fertilizations and the evolution of colonial breeding in purple martins. — Auk 107, p. 275-283.

Norris, K.J. (1990a). Female choice and the evolution of the conspicuous plumage colouration of monogamous male great tits. — Behav. Ecol. Sociobiol. 26, p. 129-138.

— — (1990b). Female choice and the quality of parental care in the great tit *Parus major*. — Behav. Ecol. Sociobiol. 27, p. 275-281.

— — (1993). Heritable variation in a plumage indicator of viability in male great tits *Parus major*. — Nature 362, p. 537-539.

Perreault, S., Lemon, R.E. & Kuhnlein, U. (1997). Patterns and correlates of extrapair paternity in American redstarts (*Setophaga ruticilla*). — Behav. Ecol. 8, p. 612-621.

Petrie, M. (1994). Improved growth and survival of offspring of peacocks with more elaborate trains. — Nature 371: p. 598-599.

— — & Halliday, T. (1994). Experimental and natural changes in the peacocks (*Pavo cristatus*) train can affect mating success. — Behav. Ecol. Sociobiol. 35, p. 213-217.

— —, — — & Sanders, C. (1991). Peahens prefer peacocks with elaborate trains. — Anim. Behav. 41, p. 323-331.

— — & Kempenaers, B. (1998). Extra-pair paternity in birds: explaining variation between species and populations. — Trends Ecol. Evol. 13, p. 52-58.

Ploger, B.J. & Mock, D.W. (1986). Role of sibling aggression in food distribution to nestling cattle egrets (*Bubulcus ibis*). — Auk 103, p. 768-776.

Price, T., Schluter, D. & Heckman, N.E. (1993). Sexual selection when the female directly benefits. — Biol. J. Linn. Soc. 48, p. 187-211.

Richardson, D.S. & Burke, T. (1999). Extra-pair paternity in relation to male age in Bullock's orioles. — Mol. Ecol. 8, p. 2115-2126.

Riven-Ramsey, D. (1988). Foraging and breeding behaviour of the cattle egret (*Bubulcus ibis*) in Barbados. — M.Sc. Thesis, University of the West Indies.

Roulin, A. (1999). Nonrandom pairing by male barn owls (*Tyto alba*) with respect to a female plumage trait. — Behav. Ecol. 10, p. 688-695.

— —, Dijkstra, C., Riols, C. & Ducrest, A.L. (2001). Female- and male-specific signals of quality in the barn owl. — J. Evol. Biol. 14, p. 255-266.

Saether, B.-E. (1990). Age-specific variation in reproductive performance of birds. — In: Current Ornithology (D.M. Power, ed.). Plenum Press, New York, p. 251-283.

Sheldon, B.C. (1994). Male phenotype, fertility, and the pursuit of extra-pair copulations by female birds. — Proc. Roy. Soc. London B 257, p. 25-30.

Trivers, R.L. (1972). Parental investment and sexual selection. — In: Sexual selection and the descent of man 1871-1971 (B. Campbell, ed.). Aldine, Chicago, p. 136-179.

Voltura, K.M., Schwagmeyer, P.L. & Mock, D.W. (2002). Parental feeding rates in the house sparrow, *Passer domesticus*: Are larger-badged males better fathers? — Ethology 108, p. 1011-1022.

Westneat, D.F. (1990). Genetic parentage in indigo buntings: a study using DNA fingerprinting. — Behav. Ecol. Sociobiol. 27, p. 67-76.

Wetton, J.H., Burke, T., Parkin, D.T. & Cairns, E. (1995). Single-locus DNA fingerprinting reveals that male reproductive success increases with age through extra-pair paternity in the house sparrow (*Passer domesticus*). — Proc. Roy. Soc. London B 260, p. 91-98.

Yezerinac, S.M. & Weatherhead, P.J. (1997). Extra-pair mating, male plumage coloration and sexual selection in yellow warblers (*Dendroica petechia*). — Proc. Roy. Soc. London B 264, p. 527-532.

Zahavi, A. (1975). Mate selection — selection for a handicap. — J. theor. Biol. 53, p. 205-214.