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Effect of testosterone on the behaviour of Yellow-legged gulls (*Larus cachinnans*) in a high-density colony during the courtship period

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Yellow-legged gulls breed in high density areas, and the condition-dependent hypothesis suggests that birds with high physical condition can obtain breeding benefits in high-density areas because they are able to pay off the energetic costs of aggressive behaviour and territory defence. This study and others showed a relationship between aggressiveness or copulation behaviour and nest-density during the pre-laying period in gulls. The link between density and behaviour can be explained by the strong competition for space and mates. Testosterone regulates male behaviour and can play an important role in the condition-dependent hypothesis. We tested the effects of testosterone implants on male breeding behaviour. In a high-density colony, testosterone-implanted male yellow-legged gulls showed higher aggression and copulation frequencies than controls during the courtship period. In addition, these testosterone-treated birds acquired larger territories than the controls. Thus, a high testosterone level can increase individual fitness in densely populated areas given the benefits derived, on the one hand, from a large territory and, on the other, from an increased copulation rate that would guarantee the male's paternity of the chicks born in his own nest. Since testosterone increases energetic requirements, only high-quality males would be able to pay off the costs of high levels of testosterone and so obtain the benefits of breeding in high-density areas. Testosterone could therefore provide a proximate mechanism regulating nest density in gull colonies.

KEY WORDS: testosterone, birds, density of nests, sexual behaviour, copulation, aggression.

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INTRODUCTION

Most gull species nest in dense colonies and birds breeding in the central dense area have a better physical quality and higher fitness (COULSON 1968, AEBISCHER & COULSON 1990). Nevertheless, the cost and benefits of high-density breeding in birds remain unclear (DANCHIN & WAGNER 1997). The principal benefit suggested is protection from predators as nests located in more populated areas of the colony are more secure than those in less dense areas (e.g. WITTENBERGER & HUNT 1985, SIEGEL-CAUSEY & KHARITONOV 1990). In gulls, the principal costs of high-density breeding are a reduction in territory size and an increase in aggressiveness (e.g. EWALD et al. 1980, PIEROTTI 1987). In these species, territory size is an important factor in chick survival. Thus, in dense areas, small territories are associated with increased nestling mortality caused by attacks from neighbours (HUNT & HUNT 1976, EWALD et al. 1980, BUTLER & JANES-BUTLER 1982, BURGER & GOCHFELD 1996). In gulls, territory attendance and defence by means of agonistic interactions are mainly male duties (TINBERGEN 1956, PIEROTTI 1981, SOUTHERN 1981, BUTLER & JANES-BUTLER 1982). Moreover, males breeding in high-density areas must increase their mate guarding to avoid extra-pair copulation (BIRKHEAD & MØLLER 1992). The "condition-dependent hypothesis" suggests that birds with high physical condition can obtain breeding benefits in high-density areas because they are able to pay off the energetic costs of aggressive behaviour and territory defence (COULSON 1968, COULSON et al. 1982, PORTER & COULSON 1987).

Male birds breeding in high-density areas have higher testosterone levels than those breeding in low-density areas (BALL & WINGFIELD 1987; BELETSKY et al. 1990, 1992; WINGFIELD & HAHN 1994), but it remains unclear whether this relationship is causal or consequential (review in BELETSKY et al. 1995). Testosterone seems to produce a reallocation of resources, increasing energetic requirements (FEUERBACHER & PRINZINGER 1981) whilst diminishing the immune response capacity (see reviews in GROSSMAN 1985, and BESEDOVSKY & DEL REY 1996, but see BRAUDE et al. 1999). Therefore, the costs that males pay for elevated testosterone levels might depend on their quality (FOLSTAD & KARTER 1992). Testosterone in male birds stimulates the development and maintenance of sexual organs (JOHNSON 1986) and, moreover, regulates male aggressiveness, particularly in a reproductive context (see WINGFIELD et al. 1990, 1994). Thus, this androgen has a higher plasma concentration just before laying (in the courtship period), when more male-male interactions occur, and then decreases abruptly afterwards (e.g. WINGFIELD et al. 1982). Hence, testosterone can play an important role in the condition-dependent hypothesis and could be a proximate mechanism regulating nest density in colonial birds. Under this hypothesis, higher levels of testosterone could increase benefits in high-density areas during the courtship period.

In order to test whether the male yellow-legged gulls (*Larus cachinnans*) breeding in high-density areas have higher aggression rates than males in low-

density areas, we studied three colonies with different density levels. Moreover, we tested the benefits of testosterone in high-density breeding areas by manipulating plasma levels of testosterone during the courtship period.

MATERIALS AND METHODS

This study was carried out during the 1996 and 1997 breeding seasons on the Isla de Ons (42°21'05"N – 5°15'35"W, Galicia, northwest Spain), where over 3000 gull pairs breed. The 1996 sampling was part of a 2-year study on gull behaviour. During the courtship period in April 1996, we studied three breeding colonies with different nesting densities. We observed 34 ringed males continuously in 30-min blocks from hides. In each colony, we undertook 24 hr of observation over a period of 6 days (4 hr per day). The birds were sampled during the 30-day period before their individual laying date (courtship period). The gulls were sexed by body size.

Displays were registered according to Tinbergen's descriptions of the Herring gull (TINBERGEN 1959). Thus, Pecking-into-the-Ground (PG; was only recorded for each impact on the vegetation), Upright (UP; was only recorded when the bird advanced towards an opponent), Choking (CH), Oblique-cum-long-calling (OLC) and the Attack frequency (AT; pecking) were also recorded. Finally, Copulation (CO) was recorded as the number of genital contacts. We converted behavioural categories into frequencies by dividing the number of actions by the number of hours (frequency per hr) that the bird was observed in the colony.

In 1997, we implanted testosterone in male gulls. Eight males were captured before the laying date (average: 28 days; range: 16-39 days), using fish-baited clap-net traps. Sex was determined by body-size measurements and confirmed by behavioural observations. The birds were immediately implanted subcutaneously with testosterone pellets (25 mg, Organon Laboratories, Cambridge). The current study was carried out with permission from the local competent authorities and avoided causing any harm to the animals. We anaesthetised birds in the field with a small dose of inhalant anaesthetic (Metofane; Pitman-Moore; Mundelein, Illinois). The pellet was inserted through a small incision in the skin on the side between the wing and the knee, and the incision was sealed with a veterinary skin bond composed of cyanoacrylate (Vet-Seal, Braun, Melsungen, Germany). The procedure took about 4 min and the bird was alert and ready for release within 10 min. Before release birds were ringed for future identification. The cited testosterone pellets have been used previously in studies on the behaviour and ecology of the red grouse *Lagopus scoticus* (MOSS et al. 1994) and black-headed gull *Larus ridibundus* (GROOTHUIS & MEEWUISSEN 1992). In captive red grouse the pellets disappeared within 5-6 weeks (MOSS et al. 1994). Maximum plasma levels during the reproductive stage of around 3 ng/mL and 5 ng/mL have been described in western gulls (*Larus occidentalis*) and black-headed gulls respectively (WINGFIELD et al. 1982, GROOTHUIS & MEEWUISSEN 1992). In captive male yellow-legged gulls 38 mg of the same testosterone pellets produced 7.28 ng/mL (mean value; range: 5.14-9.53 ng/mL) of plasma testosterone concentration for two weeks and afterwards, the implants were removed without presenting any symptoms of special degradation (ALONSO-ALVAREZ et al. unpublished data).

Given the difficulty in capturing the gulls in the colony before laying, all males were implanted in 1997. In order to avoid implant-effect differences during the first days (see GROOTHUIS & MEEWUISSEN 1992), observation started after a minimum of 6 days from implant date. Each experimental male (T-male) was paired with another male (C-male) randomly selected from amongst ringed males with territories in the same area. C-male territories never bordered directly with T-male territories. We carried out 10 hr of observation on each pair of males (one T-male and one C-males) continuously in 1-hr blocks from hides (from 09:00 to 17:00 hr; only 1 day per pair of males). Behavioural categories were recorded as in the 1996 study and frequencies were calculated by dividing the number of actions by the number of hours that the bird was observed in the colony. Gull behaviour was dependent on the place of

observation since birds were observed in pairs in eight different places in the colony. We used the Wilcoxon matched-pairs signed-ranks test to compare the behaviour of T-males and C-males. Territory size was analysed as the mean distance to the closest nests. Distance between nests was calculated by measuring with a tape measure the distance from the centre of the nest to the centre of the neighbouring nests during the incubation period (five closest nests).

Finally, in order to remove the implant at the end of the experiment, we tried to recapture the birds during incubation, but our attempts were not successful. Thereby, since the objective of this study was to analyse the costs and benefits of high-levels of testosterone only during the courtship-period, and considering the inhibitor effect of testosterone on male parental care during the incubation or the chick-rearing period (see review in KETTERSON & NOLAN 1999), the reproductive success of these birds was not analysed.

RESULTS

Significant differences in the behavioural patterns between colonies were found during the courtship period in 1996 (Table 1). Thus, PG and UP frequencies were higher in colony A than in colonies with lower densities. Moreover, there were significant differences in the copulation frequency, with high copulation rates in colony A. There were no differences in the frequency of AT, OLC and CH between colonies. There was no difference in the studied colonies in the elapsed time between the observation date and individual laying date of the pairs observed (Kruskal-Wallis test: $\chi^2 = 2.038$, df = 2, $P > 0.1$).

In 1997, implanted males showed a higher frequency of aggressive displays than control males (Fig. 1). Thus, T-males displayed higher frequency of PG than C-males (Wilcoxon matched-pairs signed-ranks test: $Z = 1.960$, $P < 0.05$) and the same pattern was found in the UP frequency ($Z = 1.960$, $P < 0.05$). Copulation was more frequent in testosterone-treated males ($Z = 2.100$, $P < 0.05$). Moreover, T-males had a higher rate of OLC than C-males ($Z = 2.100$, $P = 0.05$). The frequency of attack and choking did not differ between the groups ($P > 0.05$ in both cases).

Table 1.

Density (nests/m^2), territory size (measured as mean distance in m to the five closest nests) and behavioural frequencies (behaviour/hr) during the courtship period in three colonies with different nest densities. Colony size is given in parentheses. Data are expressed as Mean ± SE.

	Colony			Kruskall-Wallis test	
	A (n = 8)	B (n = 15)	C (n = 11)		
Density	0.028	0.019	0.005	χ^2	P
Distance between nests	6.13 ± 0.61	7.60 ± 0.32	11.69 ± 1.59	9.24	0.01
Pecking-into-the ground (PG)	4.83 ± 1.43	3.45 ± 1.01	0.78 ± 0.46	9.24	0.01
Upright (UP)	1.01 ± 0.27	0.46 ± 0.11	0.27 ± 0.09	8.11	0.02
Attack (AT)	0.71 ± 0.21	0.34 ± 0.10	0.31 ± 0.09	3.35	0.19
Copulation (CO)	0.78 ± 0.20	0.45 ± 0.10	0.23 ± 0.07	6.33	0.04
Choking (CH)	0.65 ± 0.15	0.79 ± 0.12	0.62 ± 0.24	2.83	0.24
Oblique-with-long-call (OLC)	0.43 ± 0.11	0.37 ± 0.07	0.43 ± 0.13	0.21	0.90

The mean distance to the five closest nests was higher in the T-male nests than in control nests (Wilcoxon matched-pairs signed-ranks test: Z = 2.380, $P < 0.05$; see Fig. 2). Also, the distance of the single closest nest was higher in the T-nests than in C-nests (Wilcoxon matched-pairs signed-ranks test: Z = 2.117, $P < 0.05$; C-nests: mean = 4.06, SE = 0.29; T-nests: mean = 5.09, SE = 0.28).

There were not significant difference in the time interval between the laying date and the observation day between T-nests and C-nests (C-nests: mean = 11.64 days, SE = 1.93; T-nests: mean = 15.50 days, SE = 2.33; Wilcoxon matched-pairs

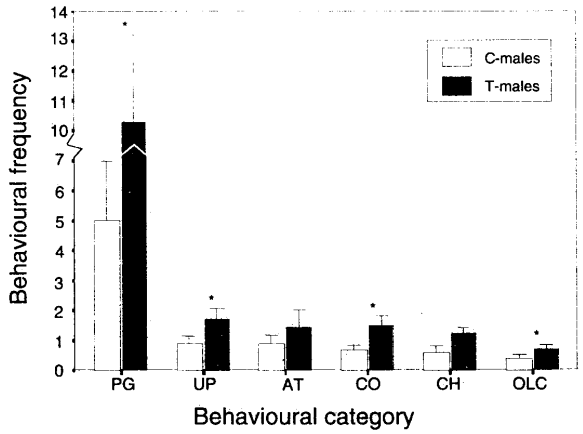


Fig. 1. — Effect of testosterone treatment (implanted males: T-males, control males: C-males, n = 8 in each group) on the behaviour of male yellow-legged gulls (behaviour/hr; Mean ± SE) frequencies in the breeding colony during the courtship period (*: $P < 0.05$). See behaviour codes in Table 1.

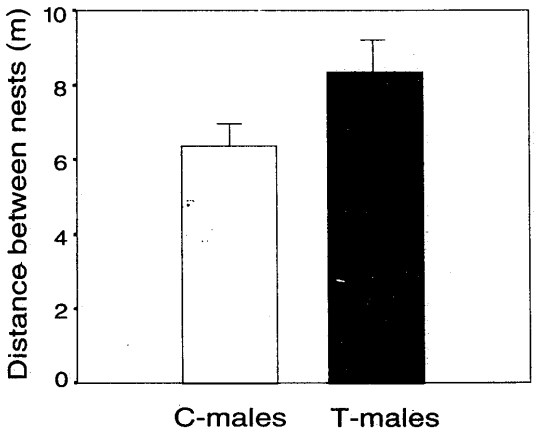


Fig. 2. — Effect of testosterone treatment (implanted males: T-males, control males: C-males, n = 8 in each group) on the territory size of yellow-legged gull (expressed as distance to the five closest nests, Mean ± SE) in the breeding colony during the courtship period.

signed-ranks test: Z = 1.069, $P > 0.1$). Neither were there differences in the laying date between testosterone treated and control pairs (Julian date: C-nests: mean = 123.75, SE = 2.49; T-nests: mean = 128.80, SE = 2.11; Z = 1.07, $P > 0.1$). The behavioural frequencies did not correlate with the laying dates ($P > 0.1$ in all cases).

DISCUSSION

This study highlights the importance of testosterone for the behaviour of yellow-legged gulls during the courtship period. Our results suggested that aggressive and sexual behaviour are more frequent in high-density colonies. The relationship between aggressiveness and nest-density during the pre-laying period has been found in other gull species (e.g. EWALD et al. 1980; BURGER 1984; PIEROTTI 1982, 1987). The link between density and behaviour in colonial birds is explained by the strong competition for space and mates (e.g. WITTENBERGER & HUNT 1985). Moreover, androgen levels correlate with breeding density in birds (BALL & WINGFIELD 1987; BELETSKY et al. 1990, 1992; WINGFIELD & HAHN 1994). In this study, we showed that testosterone influenced agonistic behaviour in high-density areas. Thus, implanted males displayed more aggressive behaviour than control males in a dense colony, specifically in UP and PG displays (Table 1). These exhibitions are related to territory acquisition and its defence (TINBERGEN 1959). In addition, T-males showed a higher OLC frequency than controls (Fig. 1), behaviour related to aggression and pair formation (TINBERGEN 1959). Our results agree with other studies showing that testosterone can increase the frequency of this display in juveniles or chicks (BOSS 1943, TERKEL et al. 1976).

Our results showed that a high plasma testosterone concentration provides some benefits. In particular, T-males increased territory size in high-density areas (Fig. 2). In gull species a bigger territory means an increase in chick survival rates (see HUNT & HUNT 1976, EWALD et al. 1980, BUTLER & JANES-BUTLER 1982, BURGER & GOCHFELD 1996). In colonial birds, this is the first study that has documented an increase in territory size after testosterone treatment, even though this has been demonstrated in two non-colonial birds (WINGFIELD 1984, MOSS et al. 1994). In the dense colony studied the testosterone implant also led to a higher rate of copulation. The effect of T on copulation frequency (Fig. 1) has not been documented in bird studies, as far as we know, despite being frequently taken for granted (review in KAST et al. 1998; but see BORGIA & WINGFIELD 1991). In spite of the fact that gulls are considered monogamous species (e.g. CRAMP & SIMMONS 1983), extra-pair copulation is a known phenomenon in these birds (MACROBERTS 1973, HUNT & HUNT 1977, MILLS et al. 1996). Thus, testosterone levels may increase the confidence in paternity by increasing copulation frequency in dense areas where there is strong competition for mates (see HUNTER et al. 1993). In conclusion, high levels of testosterone can increase male breeding fitness in high-density areas by means of territory defence and copulation behaviour.

Levels of testosterone during courtship may depend on the quality of the male. High plasma concentrations can produce an immunosuppressive effect (FOLSTAD & KARTER 1992; but see BRAUDE et al. 1999) and an increment in locomotor activity in birds (e.g. WADA 1981, GWINNER & GWINNER 1994, CHANDLER et al. 1997), which might be physiologically costly. A reduction of energetic reserves after T-treatment has also been documented (WINGFIELD 1984, KETTERSON et al. 1991).

Moreover, an experimental study showed that implanted-male birds have a lower survival rate than controls (NOLAN et al. 1992), which would be expected under this scenario. Thus in dense areas, only males in good condition could increase their fitness and pay off the energetic costs of testosterone and increased aggressive behaviour. Gulls in poor condition would not be able to support the cost of high levels of testosterone and so have fewer aggressive skills and have no option other than to breed in lower density areas. In this sense, testosterone could be a proximate mechanism regulating nest density in gull colonies.

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