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Reproductive investment and parental roles in Sabine's gulls *Xema sabini*

Abstract More than 90% of avian species exhibit biparental care, though parental activities are often shared unequally between the members of a pair. Among gull species (*Laridae*), males and females generally share parental activities, although there appear to be considerable differences between species in the relative contribution of each sex. This study examined the behaviour of male and female Sabine's gulls (*Xema sabini*) during the incubation period and immediately post-hatch; particularly the amount of time they each invested in breeding activities. Although considered an aberrant species in aspects of behaviour and biology, the Sabine's gull showed a high reproductive investment by both sexes, as other gull species do. Males fed females prior to egg laying and contributed equally to incubation and chick provisioning, and females contributed equally to nest defence. Overall, there was no difference between the sexes in the extent of their contributions to parental care, although there was considerable individual variation within pairs. Sabine's gulls are Arctic breeders and the extent of their contributions to parental activities could have been influenced by their extreme breeding environment and short breeding season.

Key words Arctic · Breeding behaviour · Parental roles · Reproductive investment · Sabine's gull · *Xema sabini*

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Introduction

Birds are unique among vertebrates, in that social monogamy is the dominant mating system (>95% of avian species; Gill 1994), and is strongly associated with biparental care (>90% of avian species; Lack 1968). Ligon (1999) suggested that the most important factor driving the prevalence of monogamy in birds is the ability to maximize the number of young reared by sharing the costs of reproduction.

In the majority of avian species, males contribute directly to the welfare of their offspring through conspicuous parental activities, such as provisioning (Ligon 1999). Avian subfamilies that are monomorphic, socially monogamous, and have altricial young, tend to show greatest male contribution to parental care (Silver et al. 1985). Nevertheless, even in strongly biparental species, parental care is not always shared equally. Based on the anisogamous nature of avian reproduction, it has generally been assumed that females make a greater contribution to the raising of offspring than males (Trivers 1972). However, where the benefits of parental care are similar for males and females, parental care activities are expected to be shared equally (Ligon 1983), although the optimal investment for each individual parent is likely influenced by the contribution provided by its mate (Houston and Davies 1985).

In seabirds, offspring survival is usually highly dependent on care by both parents (Furness and Monaghan 1987). Studies on a range of colonially nesting seabirds have shown considerable investment by both parents, and often clear sex differences in parental roles (Nelson 1978; Montevecchi and Porter 1980; Burger 1981; Pierotti 1981; Southern 1981; Butler and Janes-Butler 1983; Dulude et al. 1987; Morris 1987). For example, gull species (*Laridae*) are generally monomorphic, socially monogamous, colonial breeders, with semi-precocial or precocial young. Among the gulls, it is generally accepted that males and females share parental activities, particularly incubation, chick provisioning, and territorial defence (Morris 1987). However, among gull species, there are differences in the relative contributions of each sex to parental care activities (Dulude et al. 1987).

Sabine's gull (*Xema sabini*) is a relatively poorly known species and considered unusual within the gull family. It is recognized as phylogenetically distinct (Chu 1998), as well as being considered atypical in some aspects of its morphology (Day et al. 2001), behaviour (Brown et al. 1967) and reproductive biology (Abraham 1986; Stenhouse et al. 2001). Their breeding distribution is circumpolar and ranges from sub-Arctic to Arctic regions between 55° and 75°N (Day et al. 2001). High annual variation in breeding effort (Forchhammer and Maagaard 1991), and in predation and reproductive success (Stenhouse et al. 2003), the short duration of their breeding window, and the low opportunity for re-laying after egg loss (Day et al. 2001), all suggest that each breeding attempt is of considerable importance in an individual's lifetime reproductive success. Thus, each member of a pair is predicted to contribute to each stage of breeding, as well as contribute similar amounts of time to parental activities throughout the breeding period. In this study, we examined the behaviour of Sabine's gulls during the incubation period and immediately after hatching, with a focus on the amount of time that males and females invested in critical breeding activities, and the extent of their involvement in nest defence and chick provisioning.

Study area

Field work was conducted from late May to mid-August of 2000–2001 in the East Bay Migratory Bird Sanctuary (64°01′N, 81°47′W), Southampton Island, Nunavut, in the eastern Canadian Arctic. The East Bay sanctuary encompasses an area of approximately 1,200 km^2, and, despite being located within the Low Arctic region, is generally High Arctic in character, influenced in its ecological and physical characteristics by the deep, cold waters of the Foxe Channel. Land-fast sea ice often remains in East Bay well into July and daily minimum temperatures are close to freezing throughout summer. The study site is a 2×2.5 km area of coastal wetland tundra typical of the region. At East Bay, Sabine's gulls nest solitarily on the damp, mossy edges of small, shallow ponds or on small islands within ponds (Stenhouse et al. 2001).

Methods

Within the study area, nest searches were carried out on foot during the pre-laying and laying stages, but most nests were found only after clutch completion. The breeding behaviour of individuals and the extent to which they contributed to parental activities were explored through behavioural observations. Casual observations of Sabine's gulls in the study area were made during nest searches in the week prior to the initiation of egg laying. Once nests were established and clutches were complete, portable canvas blinds were placed ~100 m from nests, and the nesting pair (where at least one bird was banded and blood sampled) were observed with the aid of a telescope and binoculars. Obser-

vations were carried out during 3-h periods throughout the day (0800–1100 hours, 1400–1700 hours, and 1900–2200 hours). A total of 42 h of observation was achieved for two pairs in 2000, and 170 h for eight different pairs in 2001. The bulk of the observation periods ($n = 64$, 191 h) were carried out during the incubation phase, but some ($n = 7$, 21 h) were also made at five nests during hatching and the first few days of chick-rearing, referred to as the brooding phase, prior to the family's departure from the nest approximately 24 h after hatching of the last chick. In each observation period, we recorded the time each member of the focal pair was (1) incubating (on the nest), (2) present at the nest (within 3 m), (3) nearby (>3 m from the nest, but within sight), and (4) absent (out of sight), as well as all instances of incubation exchange, aggressive interaction and chick provisioning. "Anti-predator behaviour" was defined as an incubating individual leaving the nest to attack a potential predator, and "attack rate" was calculated for each individual as the number of such interactions per hour in attendance at the nest. "Provisioning rate" was calculated as the number of times per hour each parent fed chicks, based on the total hours of observation. The sex of breeding Sabine's gulls under observation was later determined from blood samples, based on the amplification of a portion of two sex-linked genes, following the procedure of Griffiths et al. (1998).

Behavioural activities, expressed as proportions of the total observation time at each nest, were compared between males and females and among pairs. Where data included repeated observations of the same birds, tests examined means or medians for each individual. There did not appear to be any difference in the breeding behaviour of Sabine's gulls between years, and data were lumped for analyses. When data did not meet the assumptions of parametric statistics, a non-parametric test, the Wilcoxon signed rank test, was used. All statistical tests were performed using Data Desk statistical software v 6.1 (Data Description, Ithaca, N.Y.). Throughout, statistical significance was recognized at $P \leq 0.05$ and tests were two-tailed. Values reported below are means ± SD, unless otherwise stated.

Results

Pre-laying phase

Qualitative observations in the week prior to egg laying showed that pairs spent increasing time associated with a particular area in which they eventually nested. Males were occasionally observed to feed females during this pre-laying period. In these instances of courtship feeding, males always regurgitated food onto the ground in front of females (cf. Brown et al. 1967), as other gulls do.

Incubation phase

Overall, there were no significant differences between males and females in the percentage of time they spent in

different behavioural activities during the incubation phase, although males appeared to show slightly more individual variation in their parental contributions than females. Both sexes spent a similar percentage of time incubating (Table 1); however, the difference among individuals varied considerably and ranged up to 44% among females (27–71% of time) and 48% among males (23–71% of time). Two pairs showed equal effort (<5% difference in the percentage of time each member spent incubating) and eight pairs showed unequal effort (>5% difference), with females incubating more in five pairs, and males more in three pairs. Time spent in incubation remained similar throughout the day and there were no statistical differences between females and males in each time period (Table 2). The duration of incubation shifts were also similar for females (66 ± 13 min, $n = 7$) and males (51 ± 13 min, $n = 7$), and there was no difference in the mean length of incubation shifts between the sexes (two sample t-test, $t = 1.74$, $P = 0.10$). On nine occasions, birds were observed incubating for a complete observation period (≥ 3 h); six involving females and three involving males. Besides incubating, females and males spent very little time at the nest, little time nearby, and similar time absent from the nest area (Table 1). However, the difference between individuals in the proportion of time they were absent varied considerably and ranged up to 39% (23–62% of time) among females and 45% (21–66% of time) among males.

Anti-predator behaviour was similar in both sexes during the incubation period (Table 1). Overall, there was no association between time spent in incubation and the number of times birds left the nest to attack ($r_s = 0.22$). Furthermore, there was no difference in the proportion of potential predatory threats (i.e. the presence of a predator in the area) that incubating females (0.81 ± 0.16, $n = 8$) and males (0.77 ± 0.26, $n = 10$) responded to (Wilcoxon signed rank test, $P = 0.84$).

Of the ten pairs observed, only one was unsuccessful, due to egg predation at day 19 of incubation. This is similar to the success rate (0.8) at ten randomly selected unobserved nests from the same years (two in 2000, eight in 2001), suggesting that the presence of observation blinds had little negative impact on observed pairs. The unsuccessful observed pair showed no apparent behavioural differences compared to successful pairs.

Brooding phase

In general, there were no significant differences between females and males in the time they spent in different behavioural activities during the early brooding phase, although females appeared to show slightly more individual variation in their parental contributions than males. There was no statistical difference between females and males in the mean time spent brooding chicks (Table 3). However, the

Table 1. Mean ($\pm$ SD) percentage of total observation time spent in activities and attack rate for female ($n = 10$) and male ($n = 10$) Sabine's gulls breeding at East Bay, Nunavut, Canada, during the incubation period, and the results of tests comparing the sexes ($T = $ Wilcoxon signed rank test, $t = t$-test)

Behaviour	Female mean	SD	Male mean	SD	Test	P
Incubation	51.1	16.1	45.8	16.6	T	0.85
At nest	0.2	0.2	0.7	1.5	T	0.94
Nearby	9.7	8.4	14.4	12.4	T	0.92
Absent	39.1	13.2	39.3	15.6	T	0.49
Attack rate	0.51	0.37	0.57	0.35	t	0.87

Table 2. Mean ($\pm$ SD) percentage time spent in incubation throughout the day by female and male Sabine's gulls breeding at East Bay, Nunavut, Canada, and the results of Wilcoxon signed rank tests comparing the sexes

Time period	Female n	Mean	SD	Male n	Mean	SD	z	P
0800–1100	22	49	31	22	46	32	0.36	0.72
1400–1700	33	49	26	33	45	28	0.33	0.73
1900–2200	16	56	22	16	41	21	0.96	0.34

Table 3. Mean ($\pm$ SD) percentage of total observation time spent in activities, attack and provisioning rates for female ($n = 5$) and male ($n = 5$) Sabine's gulls breeding at East Bay, Nunavut, Canada, during the brooding period, and the results of tests comparing the sexes ($T = $ Wilcoxon signed rank test, $t = t$-test)

Behaviour	Female mean	SD	Male mean	SD	Test	P
Brooding	37.0	22.7	50.4	21.9	T	0.44
At nest	2.3	1.7	4.9	4.9	T	0.38
Nearby	25.0	15.1	29.0	9.7	T	0.19
Absent	39.2	23.9	19.2	9.3	T	0.88
Attack rate	0.17	0.16	0.30	0.24	t	0.82
Provisioning rate	0.70	0.45	0.70	0.18	t	0.56

difference among individuals in time spent on the nest varied considerably, and ranged up to 34% (19–53% of time) among females and 52% (24–76% of time) among males.

Parents spent little time at the nest, but they spent more time nearby than during the incubation phase (Table 3), largely due to short-range foraging bouts around the nest to provision chicks. Females were absent from the nest area as much as during the incubation phase, and while males were absent for considerably less time than during the incubation phase, there was no statistical difference in their absence between phases (Table 3; Wilcoxon sign rank test, $P = 0.12$). There were also no differences in the mean attack or provisioning rates. Although the anti-predator behaviour of both sexes appeared lower during brooding than in the incubation phase, there were no significant differences between phases (females, $t = -0.48$, $P = 0.65$; males, $t = 0.36$, $P = 0.73$).

Discussion

It has been suggested that females carry a greater burden of reproduction (Trivers 1972). However, as is expected among monogamous, biparental pairs, the males of most gull species invest heavily in the production of their young, contributing to the formation of the clutch and other critical parental activities (Pierotti 1981; Butler and Janes-Butler 1983; Dulude et al. 1987).

In general, Sabine's gulls appear to exhibit a fairly typical gull pattern in their breeding behaviour (i.e. both sexes exhibit a high reproductive investment and share parental activities), although there was considerable individual variation within pairs. Despite an unequal division of time spent in incubation in some pairs, nest attendance by at least one parent was very high at all nests (94–98%) over the incubation phase, and hatching success at East Bay was relatively high in both years of this study. In some large gull species, males are often more involved in anti-predator interactions and nest defence than females (Southern 1981; Morris and Bidochka 1982; Hand 1986), but this was not the case in Sabine's gulls. However, the early departure from the nest so soon after hatching is particularly notable and may reflect the high risk of nest predation in some years (Stenhouse et al. 2003). Although Sabine's gulls attend their chicks after leaving the nest (Day et al. 2001), the roles of parents and the division and duration of parental activities during this period remain unknown. Overall, the particularly high degree of parental care exhibited by both sexes of Sabine's gulls in this study could have been influenced by the pressures of a short breeding season (Day et al. 2001) and the high risk of predation at the nest in some years (Stenhouse et al. 2003).

Clearly, a lack of statistically significant difference between two samples does not mean that the two samples can be considered identical. Sample sizes were admittedly low throughout this study, particularly during the brooding phase, thus, statistical power was also low. Increasing sample sizes would increase the power of statistical tests (Steidl

et al. 1997), and could potentially lead to statistically significant results. Although the differences between females and males in general (i.e. the effect sizes) were slight, the differences among individuals of both sexes were considerable. Thus, even if differences between females and males do exist, the difference would probably only explain a small portion of the variance compared to the among-individual variation caused by factors other than sex.

The extent of individual variation in parental contributions within Sabine's gull pairs is perhaps the most interesting result from this study and is particularly intriguing. Ideally, it would be enlightening to relate the variation in the division of parental activities within pairs to their reproductive success (see Morris 1987). However, hatching success in Sabine's gulls was high in both years of this study, and sample sizes were low, precluding such investigation. A thorough examination of the influence of individual variation on fitness would require a considerably longer-term study, increased sample sizes, and inclusion of years of high reproductive failure (e.g. due to egg predation). It is during "poor" reproductive years that variation in the division of critical parental activities, such as incubation and nest defence, would be predicted to be most influential and evident.

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