SEXUAL DIFFERENCES IN THE BEHAVIOR OF ADULT GREAT BLACK-BACKED GULLS (*LARUS MARINUS*) DURING THE PRE- AND POST-HATCH PERIODS

RONALD G. BUTLER[1] AND SASKIA JANES-BUTLER

The Mount Desert Island Biological Laboratory, Salsbury Cove, Maine 04672 USA

ABSTRACT.—Sexual differences in the behavior of adult Great Black-backed Gulls (*Larus marinus*) were examined during the pre- and post-hatch periods of the 1980 breeding season. Following clutch completion, females invested more time than males in both territorial attendance and incubation, but there were no sexual differences in egg-shifting or grass-collection. In contrast, males engaged in more agonistic behavior and long-called and yelped in all contexts more than females before chick hatching. Males also displayed more mate-oriented mews and chokes than did females at this time. During the post-hatch period, there were no sexual differences in territorial attendance, brooding, or frequency of chick feedings, but males continued to exhibit higher frequencies of agonistic acts than did females, as well as higher levels of long-calls and yelps. After chick hatching, both sexes demonstrated increased levels of agonistic acts, long-calls, yelps, mews, and yeows, while males exhibited decreased frequencies of chokes and head-tosses. The results of this study strongly suggest that parental investment by male *L. marinus* may equal that of females. *Received 10 August 1981, accepted 28 May 1982.*

GULL species (Laridae) are generally monogamous, and members of both sexes exhibit the same behavior patterns related to parental care during the breeding season (e.g. incubation, brooding, chick feeding, territorial attendance and defense). Male and female gulls are often difficult to distinguish visually, and many descriptions of their behavioral ecology have simply "lumped" sexes in data analysis. Recent studies, however, have shown that definite differences are evident in the behavior of male and female larids. For example, Tinbergen (1956, 1960) reported that male Herring Gulls (*Larus argentatus*) were more active in collecting nest material and were involved in territorial defense more often than females. Similarly, male and female Laughing Gulls (*L. atricilla*; Burger and Beer 1975) and Ring-billed Gulls (*L. delawarensis*; Southern 1981) have been observed to exhibit differences in agonistic behavior toward territorial intruders. Male Western Gulls (*L. occidentalis*) are not only responsible for the bulk of territorial defense, but also

feed chicks significantly more often than do females (Pierotti 1981). Burger (1981a) reported that, although adult male and female Herring Gulls contribute equal parental investment in the post-hatch period, sexual differences in investment patterns developed as chicks grew older. Even sexual differences in spiteful and altruistic behavior have been observed in both Herring and Western gulls (Pierotti 1980). Clearly, the investment patterns of adult larids vary qualitatively, if not quantitatively, and additional data are needed to evaluate the relative significance of male and female contributions in terms of parental effort.

We examined the behavior of adult Great Black-backed Gulls (*L. marinus*) during the incubation and post-hatch phases of the reproductive cycle. The specific objectives of this study were to: (1) investigate possible sexual differences in a number of agonistic and non-agonistic behaviors exhibited by breeding adults and (2) determine how the transition from the pre- to post-hatch periods influenced the behavior of males and females.

METHODS

This study was conducted on Little Duck Island, Hancock County, Maine between April and August 1980. Approximately 520 pairs of *L. marinus* nested

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[1] Present address: Department of Biological Sciences, Duquesne University, Pittsburgh, Pennsylvania 15282 USA.

TABLE 1. Sexual dimorphism in Great Black-backed Gulls.[a]

Sex	Weight (g)	Tarsus (mm)	Culmen (mm)	Bill depth at nares (mm)
Males (n = 19)	1,963 ± 11[b]	97.9 ± 0.4[b]	66.1 ± 0.6[b]	25.4 ± 0.2[b]
Females (n = 11)	1,577 ± 19	90.7 ± 0.7	59.7 ± 0.4	22.2 ± 0.1

[a] Data expresses as mean ± SE.
[b] Males > Females in t-test comparison, P < 0.001.

in two large meadows on this 35-ha island. Breeding habitat consisted of several species of grasses (*Gramineae*), stinging nettle (*Urtica dioica*), angelica (*Angelica lucida*), raspberry (*Rubus idaeus*), and exposed granite outcroppings. The island was uninhabited and supported no mammalian predators.

A blind was erected on masonary scaffolding at the periphery of the colony during the pre-incubation stage of the Great Black-backed breeding cycle. One or both adults on each of 19 nest sites were color marked with leg-streamers during the 1978, 1979, and 1980 breeding seasons (and all adults were marked with temporary dyes), all pairs were sexed on the basis of size differences, and sexes were confirmed through observed copulations. In all 19 cases, the larger member of the pair was a male, and morphometric data (see Table 1) indicated sexual dimorphism similar to that reported by Ingolfsson (1967). Study nests were selected to include sites from both high- and low-density areas within the colony (Butler and Trivelpiece 1981). Data were collected only from those territories that were entirely visible for the duration of the breeding season and those in which both members of the pair were in attendance until chicks fledged. Chicks were considered fledged at 55 days following hatching and/or when they were observed flying strongly in the vicinity of the colony.

Behavioral observations of birds on their nesting territories were conducted during daylight hours (0500–2100) over the course of the breeding season. Two observers watched an average of 10 territories on each of 18 days (1,877 nest hours) during the pre-hatch period and an average of 7 territories during 20 days (1,701 nest hours) of the post-hatch period. We recorded the frequencies and identities of adults engaged in the following behaviors (where necessary, definition or source of previous description for other gull species noted): upright aggressive (Fig. 1a; Moynihan 1958), grass-pull (Tinbergen 1959, 1960), face-off (behavior that occurred in an agonistic context in which one or more adults assumed a recumbant position oriented either facing or parallel to a neighboring conspecific within 1 m of a territorial boundary, possibly related to a squat-and-freeze described by Moynihan 1958), jab (gaping-jab of Moynihan 1958), charge (lunge or running approach by an adult with wings generally extended; charging bird always terminated behavior before making contact with another conspecific), chase (aerial pursuit of one adult by another), attack (physical assault upon one adult by another, which generally involved biting), fight (prolonged bout of mutual attacking), long call (Fig. 1b; Moynihan 1958, Tinbergen 1959), yelp (Fig. 1c; Stout et al. 1969, Hand 1981), mew (Fig. 1d; Tinbergen 1959, Hand 1981), yeow (plaintive call of Moynihan 1958, plaintive yeow of Hand 1981), gakker (Moynihan 1958, Eh-Eh call of Hand 1981), choke (Fig. 1e; Moynihan 1958, Tinbergen 1959), head-toss (Fig. 1f; Hand 1981), shift or roll eggs, grass-collect, feed chick, present grass to chick, and reconsume regurgitated food. In addition, the frequency and duration of time on the territory, incubation bouts, and brooding bouts were noted. Data collection was facilitated by our use of binoculars (10×), digital stopwatches, cassette tape-recorders, and super-8 mm movie cameras. We determined territorial boundaries by means of aerial photographs taken in May 1980 and measurements made with an optical tape measure (see Butler and Janes-Butler 1982).

For the purpose of examining sexual differences in behavior, frequency scores from each adult pair were analyzed using the Wilcoxon signed-ranks test. Intrasexual comparisions between the pre- and post-hatch periods were analyzed in the same fashion. Proportional differences were treated with the Chi-square statistic applied to raw data rather than percentages. Morphometric data were analyzed using the t-test. To facilitate analysis and discussion, behavioral data were broken down into acts related either to attendance and care of offspring, intrapair behavior, or agonistic interactions. Behaviors such as the long-call, which occurred in each of the above categories, were analyzed according to their contextual appearance.

RESULTS

Attendance and care of offspring.—Before their chicks hatched, adult females were observed occupying territories (t = 51.1, n = 19, P < 0.05) and incubating (t = 32.0, n = 19, P < 0.005; Fig. 2) significantly more than were males. There were no differences, however, between males and females in the mean (±SE) frequencies of egg-shifting ($\bar{x}$ = 0.30 ± 0.05/h
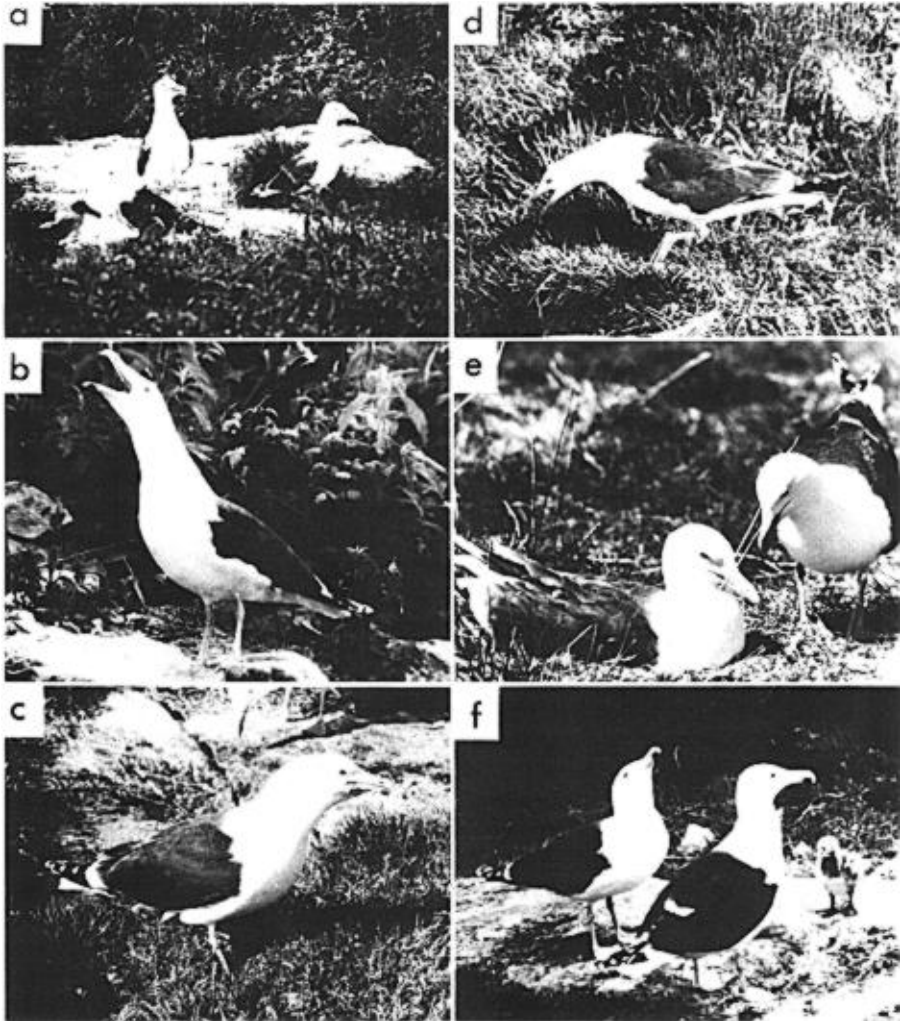
Fig. 1.   Behavior patterns in which male and female Great Black-backed Gulls differed over the course of the breeding season: (a) upright aggressive (and gakker) by several adults near territorial boundary, (b) long-call, (c) yelp, (d) mew, (e) choke by pair following grass presentation by standing bird, (f) head-toss (adult female on left) before regurgitation by mate to chick.

and 0.34 ± 0.04/h, respectively) or bouts of nest-substrate collecting ($\bar{x}$ = 0.18 ± 0.05/h and 0.14 ± 0.08/h, respectively). The mean nest-relief interval was 5.3 ± 0.6/h, and males fed females at the nest site only infrequently following clutch completion ($\bar{x}$ = 0.007 ± 0.006/h). Following chick hatching, males and females did not differ in terms of time in attendance on the territory, and both sexes participated equally ($\bar{x}$ = 13 ± 5 min/h and 18 ± 5 min/h, respectively) in brooding chicks during the first week following hatching (Fig. 2).

Males and females did not differ significantly in terms of which hours of the day they were in attendance during either the pre- or post-hatch periods. The overall adult attendance pattern did change, however, following hatching (Fig. 3). During the pre-hatch period, maximum numbers of adults were in attendance on territories during early morning, late afternoon, and evening hours, and territories were generally left unattended for no longer than 1–2 min. During these brief absences, the adult in attendance generally flew out over the col-
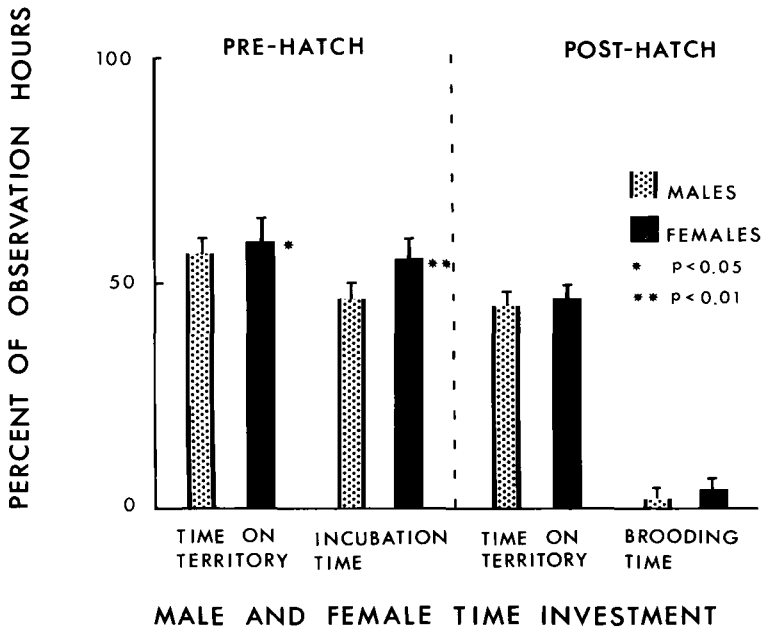
Fig. 2.   Pre-hatch (1,877 nest-hours) and post-hatch (1,701 nest-hours) comparisons of male and female time investment in territorial attendance, incubation, and brooding. Significant Chi-square values for intersexual comparisons (*) are indicated.

ony, defecated, and then returned to incubate. In contrast, during the post-hatch period, one or sometimes both mates left the territory in early morning (presumably to forage to feed their chicks), and maximal numbers of adults were observed on the territories only in late afternoon and evening. Temporary adult desertion of territories increased steadily from 0.2% of the total observation hours in the first 10 days of June to 46.3% of the observation hours in the last 10 days of July. Some chicks were left unattended for periods of up to 8 h, and presumably both adults were out foraging at these times. Although this pattern varied between high- and low-density nesting areas (Butler and Janes-Butler 1982), there were no sexual differences in the proportion of time spent away from the territory by pairs in these areas. Attendance patterns during both the pre- and post-hatch periods in 1980 were not affected significantly by the occurrence of high and low tides. This may be related to the fact that, during 1980 breeding season, over 87% of the food items identified (47% of all chick feedings) consisted of fish [alewife (*Pomolobus pseudoharengus*), herring (*Clupea harengus*),

lumpfish (*Cyclopterus lumpus*), mackeral (*Scombar scombrus*), sculpin (*Myoxocephalus* sp.), and unidentified fish remains] or pelagic invertebrates [krill species and squid (*Loligo borealis*)], organisms relatively independent of tidal cycles. There were no sexual differences in the types of food items fed to chicks. Males and females did not differ in mean frequencies of chick feedings ($\bar{x} = 0.50 \pm 0.06$/h and 0.45 ± 0.06/h, respectively), reconsumption of food offered to chicks ($\bar{x} = 0.12 \pm 0.04$/h and 0.13 ± 0.03/h, respectively), or presentation of grass or other substrate to chicks ($\bar{x} = 0.13 \pm 0.03$/h and 0.17 ± 0.05/h, respectively).

Adult vocalizations that were directed at chicks included long-calls, mews, and yelps. Chicks that mandibulated the bills of recumbant adults and/or continuously solicited feedings often elicited long-calls from their parents. Adults also long-called when chicks left the territory and/or when they returned to the territory, especially if neighboring adults were in the area. Males long-called more than females in this context ($t = 32.5$, $n = 19$, $P < 0.01$). Adults yelped and mewed most often before feeding chicks. These vocalizations were also
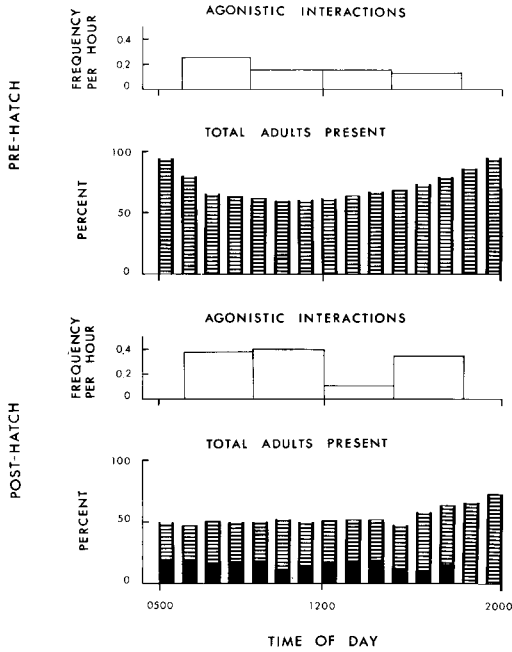
Fig. 3.   Diurnal changes in both territorial attendance (expressed as percentage total adults in attendance) and the mean frequencies of agonistic acts for adult gulls during the pre- and post-hatch periods. Blackened portions of attendance bars represent percentage of territories left unattended during the post-hatch period.
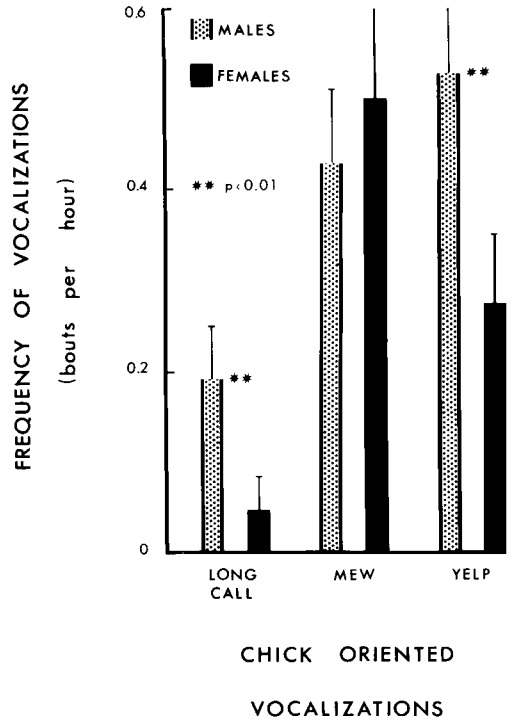

CHICK   ORIENTED

VOCALIZATIONS

Fig. 4.   Comparisons of mean frequencies of chick-oriented vocalizations exhibited by adult males and females. Results of Wilcoxon signed-ranks tests for intersexual comparisons (*) are indicated.

used by adults, however, when chicks were out of sight in dense vegetation or when chicks wandered too close to a territorial boundary or a neighboring adult. Males yelped significantly more often than females ($t = 29.5$, $n = 19$, $P < 0.01$), but there were no sexual differences in the frequency of chick-oriented mews (Fig. 4).

Pair-bond related behavior.—Adults directed long-calls, mews, yelps, chokes, and head-tosses at their mates during both the pre- and post-hatch periods (Fig. 5). Long-calls were generally given to or by landing mates, and males long-called more than females during both the pre-hatch ($t = 35.0$, $n = 19$, $P < 0.01$) and post-hatch periods ($t = 41.5$, $n = 19$, $P < 0.025$). Both males and females exhibited increased frequencies of mate-directed long-calls following chick hatching ($t = 30$, $n = 19$, $P < 0.005$ and $t = 0$, $n = 19$, $P < 0.005$, respectively). Mate-oriented mews and chokes, and to a lesser extent head-tosses, appeared primarily in the context of nest relief in both sexes. Head-tossing also appeared in the context of limited

mate feeding during the early pre-hatch periods, as well as during attempts by females to eat food being presented by males to their chicks during the post-hatch period. There were no sexual differences in head-tossing during the pre-hatch period (Fig. 5), but males mewed ($t = 46.0$, $n = 19$, $P < 0.025$) and choked ($t = 28.5$, $n = 19$, $P < 0.01$) more than their mates. Both sexes exhibited significant decreases in mate-directed mews following hatching (males: $t = 13.0$, $n = 19$, $P < 0.005$; females: $t = 18.0$, $n = 19$, $P < 0.005$), but only males choked ($t = 53.5$, $n = 19$, $P < 0.05$) and head-tossed significantly less frequently ($t = 25$, $n = 19$, $P < 0.005$) during this period. Finally, males and females yelped before their own or their mate's aerial departure from the territory. Males yelped in this context significantly more often than females, however, both before ($t = 19.5$, $n = 19$, $P < 0.005$) and after ($t = 11.5$, $n = 19$, $P < 0.005$) chick hatching. Intrasexual comparisons of yelps before and after hatching revealed no significant changes (Fig. 5).
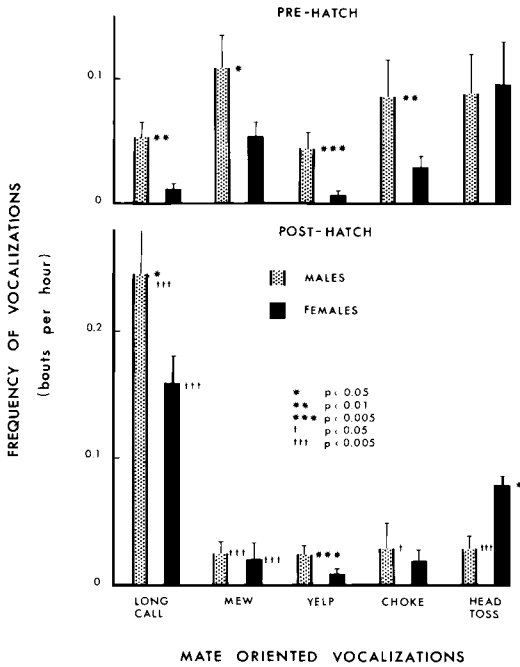
Fig. 5. Pre- and post-hatch comparisons of mean frequencies of mate-oriented vocalizations exhibited by adult males and females. Results of Wilcoxon signed-ranks tests for intersexual comparisons (*) and intrasexual comparisons between the pre- and post-hatch periods (†) are indicated.
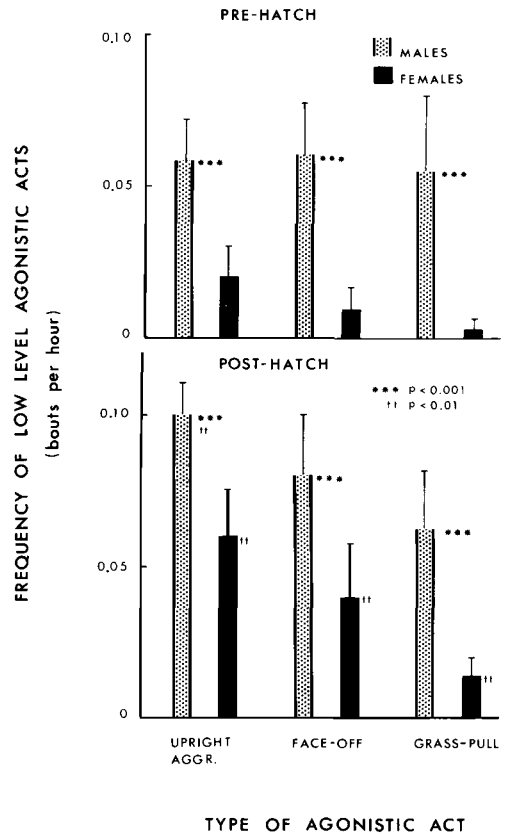

Fig. 6. Pre- and post-hatch comparisons of the mean frequencies of low-level agonistic acts by adult males and females. Results of Wilcoxon signed-ranks tests for both intersexual comparisons (*) and intrasexual comparisons between the pre- and post-hatch periods (†) are indicated.

Agonistic behavior.—Agonistic interactions accounted for 34% of all social interactions during the pre-hatch period and 35% of all encounters during the post-hatch period. Males and females exhibited marked sexual differences in agonistic behavior during both periods (Fig. 6 and 7). During the pre-hatch period, males exhibited significantly greater frequencies of low-level agonistic acts than did females, including upright aggressive displays ($t = 13.5$, $n = 19$, $P < 0.001$), face-off encounters ($t = 12.0$, $n = 19$, $P < 0.001$), and grass-pulling bouts ($t = 12.0$, $n = 19$, $P < 0.001$; Fig. 6). There were no statistical differences in frequencies of high-level agonistic acts in the pre-hatch phase of the breeding cycle. During the post-hatch period, males again displayed significantly greater frequencies of upright aggressive behavior ($t = 27.5$, $n = 19$, $P < 0.01$), face-off interactions ($t = 36.5$, $n = 19$, $P < 0.01$), and grass-pulling bouts ($t = 12.0$, $n = 19$, $P < 0.001$; Fig. 6). Males also charged conspecifics significantly more often than did fe-

males ($t = 36.0$, $n = 19$, $P < 0.01$), although there were no other significant differences in frequencies of high-level agonistic acts following chick hatching (Fig. 7). The frequency of fights that males ($\bar{x} = 0.005 \pm 0.004$/h) and females ($\bar{x} = 0.002 \pm 0.002$/h) engaged in did not differ significantly.

Intrasexual comparisons of the pre- and post-hatch phases indicated that, following hatching, males demonstrated significantly higher levels of upright aggressive behavior ($t = 28.5$, $n = 19$, $P < 0.005$), charges $t = 35.5$, $n = 19$, $P < 0.01$), and chases ($t = 0$, $n = 19$, $P < 0.001$; Figs. 6 and 7). Females showed changes only in the frequency of low-level agonistic acts during the post-hatch period. These included significant increases in upright aggressive acts ($t = 18.5$, $n = 19$, $P < 0.005$), face-off behav-
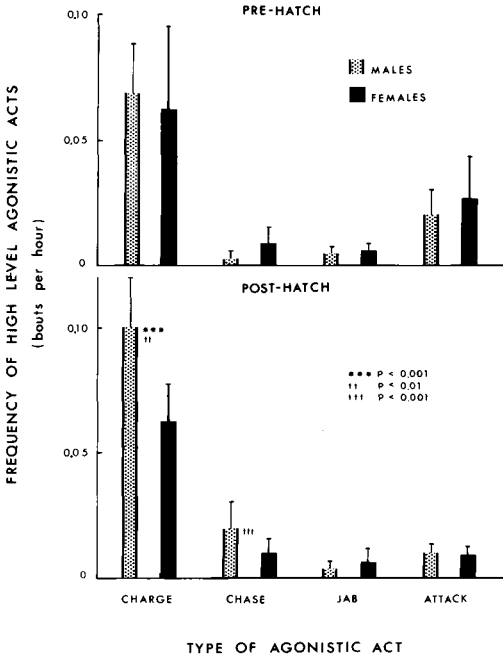
Fig. 7. Pre- and post-hatch comparisons of the mean frequencies of high-level agonistic acts for adult males and females. Results of Wilcoxon signed-ranks tests for both intersexual comparisons (*) and intrasexual comparisons between the pre- and post-hatch periods (†) are indicated.
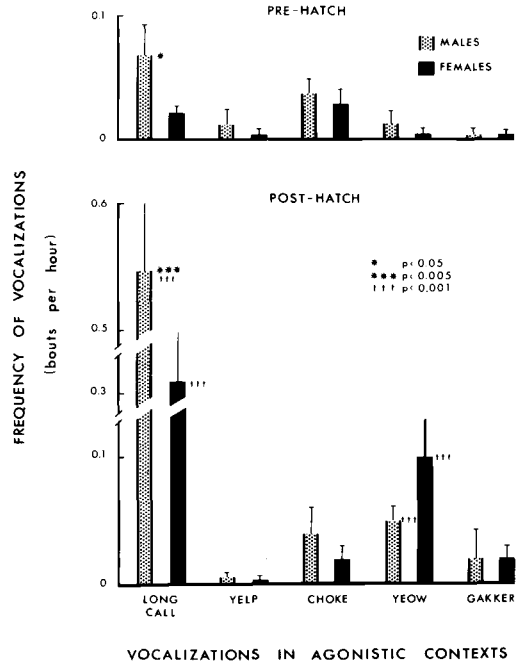

Fig. 8. Comparisons of pre- and post-hatch mean frequencies of vocalizations that were exhibited by adult males and females in agonistic contexts. Results of Wilcoxon signed-ranks tests for both intersexual comparisons (*) and intrasexual comparisons between the pre- and post-hatch periods (†) are indicated.

ior ($t = 36.5$, $n = 19$, $P < 0.01$), and grass-pulling ($t = 25.0$, $n = 19$, $P < 0.01$; Fig. 6). The frequencies of agonistic behavior displayed by both sexes showed an abrupt and sustained increase over the course of the entire post-hatch period. Examination of the daily occurrence of agonistic interactions from 0600 to 0900, 0900 to 1200, 1200 to 1500, and 1500 to 1800 revealed no substantial differences during the pre-hatch period (Fig. 3). Following hatching, however, a distinct decrease in agonistic interactions for both sexes was observed between 1200 and 1500 (Fig. 3). This decrease corresponded to generally higher ambient temperatures and the tendencies for both adults and chicks to sleep or remain inactive during these periods.

Vocalizations that were frequently exhibited by adult gulls in agonistic contexts included the long-call, yelp, choke, yeow, and gakker. The long-call, yelp, and choke occurred most frequently during conspecific overflights of the territory, during interactions involving adjacent territory holders, when a neighboring

adult landed on its own territory, when other adults gave long-calls or yelps, when two or more neighboring territory holders that shared a common boundary with a calling gull interacted, or at times in response to a non-neighboring intruder before a more high-level response by the territory holder. The yeow and gakker, which appeared to function more as alarm or alerting calls, were observed most often when a high-level agonistic interaction was in progress near the territorial boundary of the calling bird, when adults and chicks from two different territories were in close proximity near their mutual boundaries, when the calling bird's chick was in an adjacent territory, when a calling bird was intruding into an adjacent territory, or on windy days when large numbers of adults were soaring over a calling gull's territory. During the pre-hatch period, males displayed significantly higher frequencies of long-calls than their mates ($t = 51.5$, $n = 19$, $P < 0.05$) but did not differ with regard to oth-
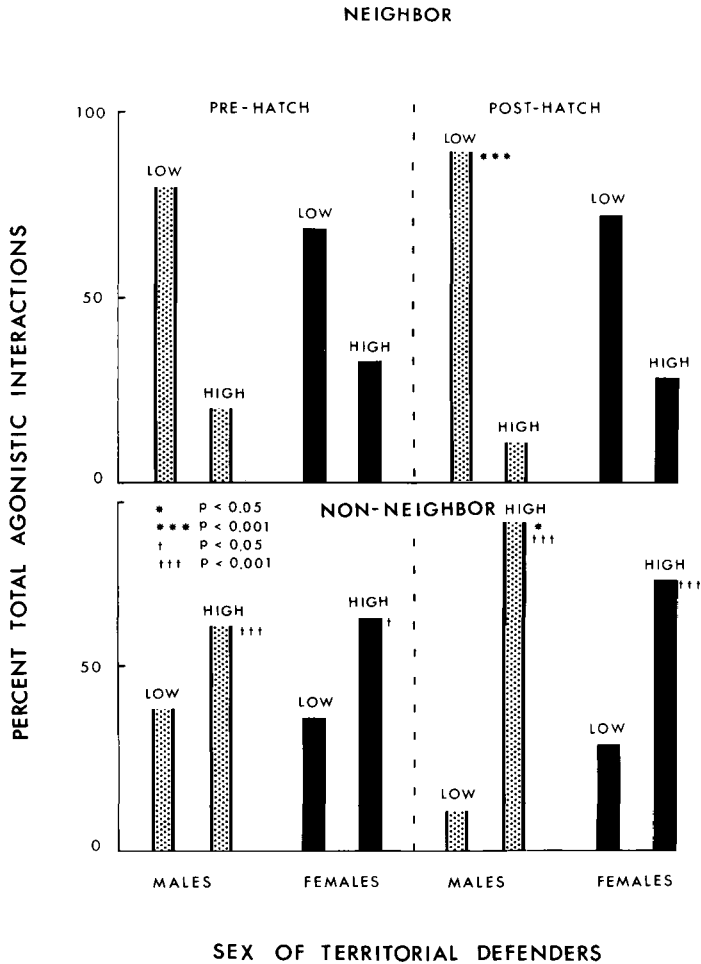
Fig. 9. Percentage of low- and high-level agonistic interactions between neighboring and non-neighboring intruders and adult males (total of 442) and females (total of 192), during the pre- and post-hatch periods. Results of Chi-square tests for both intersexual comparisons (*) and intrasexual comparisons between the pre- and post-hatch periods (†) are indicated.

er agonistic vocalizations (Fig. 8). Similarly, during the post-hatch period, males showed significantly higher frequencies only of long calls ($t = 4.0$, $n = 19$, $P < 0.001$). Both males and females displayed intrasexual increases in the frequencies of both long-calls (males: $t = 0$, $n = 19$, $P < 0.001$; females: $t = 0$, $n = 19$, $P < 0.001$) and yeows (Males: $t = 12$, $n = 19$, $P < 0.001$; females: $t = 11$, $n = 19$, $P < 0.001$) following chick hatching (Fig. 8).

Males and females also displayed some differences in agonistic behavior related to territorial defense, depending on both the sex and type of intruder (i.e. neighbor or non-neigh-

bor). Both males and females displayed significantly more high-level agonistic responses to non-neighboring intruders than to neighboring intruders during both pre- ($\chi^2 = 29.56$, df $= 1$, $P < 0.001$ and $\chi^2 = 6.06$, df $= 1$, $P < 0.05$, respectively) and post-hatch periods ($\chi^2 = 147.22$, df $= 1$, $P < 0.001$ and $\chi^2 = 26.07$, df $= 1$, $P < 0.001$, respectively; Fig. 7). During the post-hatch period, however, males displayed a significantly greater proportion of low-level responses to neighbors ($\chi^2 = 11.58$, df $= 1$, $P < 0.001$) and high-level responses to non-neighbors ($\chi^2 = 4.68$, df $= 1$, $P < 0.05$) than did females (Fig. 9). Comparisons of the pre- and
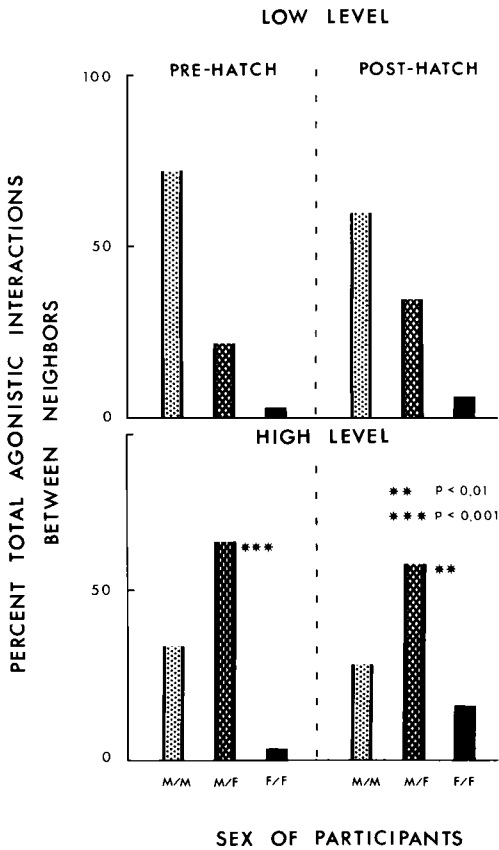
Fig. 10. Percentage of low- and high-level territorial interactions that occurred between three possible dyads; M/M = male-male (240 interactions), M/F = male-female (147 interactions), F/F = female-female (27 interactions). Results of Chi-square tests of comparisons (*) of the distribution of low- and high-level interactions between the pre- and post-hatch periods are indicated.

post-hatch periods revealed no significant changes in the frequencies of intrusions by either neighboring ($\bar{x}$ = 0.12 ± 0.03/h and 0.16 ± 0.04/h, respectively) or non-neighboring conspecifics ($\bar{x}$ = 0.08 ± 0.02/h and 0.10 ± 0.03/h, respectively).

Analysis of agonistic interactions between neighboring territorial adults (in which the sexes of both members of a dyad could be identified) indicated that, during the pre- and post-hatch periods, low-level agonistic interactions occurred primarily between males and high-level encounters occurred most often between male and female defenders (χ^2 = 14.89, df = 1, P < 0.001 and χ^2 = 11.93, df = 1, P <

0.01, respectively; Fig. 10). Female-female interactions were rare and accounted for only 6% of the agonistic encounters between neighboring pairs. These data reflect the type of response directed at approaching males and females by defenders of the same or opposite sex regardless of the phase of the breeding cycle. Males approaching or intruding within a territorial boundary generally elicited a low-level agonistic act from defenders of either sex. Approaching or intruding females, however, were significantly more likely to stimulate a high-level response (e.g. attack, charge, or chase) by both males (χ^2 = 19.69, df = 1, P < 0.001) and females (χ^2 = 5.16, df = 1, P < 0.05; Fig. 11).

Pre- and post-hatch comparisons of male and female reactions to the involvement of their mates in an agonistic interaction (while both members of the pair were in attendance) revealed significant increases in the proportion of agonistic responses by both males (χ^2 = 6.46, df = 1, P < 0.05) and females (χ^2 = 6.03, df = 1, P < 0.05). In addition, males were much more likely to exhibit agonistic responses to aggressive interactions involving their mates than were females (χ^2 = 4.93, df = 1, P < 0.01). Male involvement in these mate-neighbor interactions was often closely preceded or followed by the female mate's withdrawal and mewing return to the vicinity of the chicks. Intermate agonistic interactions were infrequent and generally involved a male attacking its mate as she attempted to eat food regurgitated by the male to its chicks. Females were never observed attacking their mates under similar circumstances.

DISCUSSION

The results of the present study of adult Great Black-backed Gulls indicate that: (1) females invested more time than males in territorial attendance and incubation during the pre-hatch period; (2) there were no sexual differences in other types of offspring care or in territorial attendance during the post-hatch period; (3) males were more aggressive than females throughout the season; (4) both males and females displayed increased investment in agonistic behavior during the post-hatch period, as well as increased levels of long-calls and yeows in agonistic contexts; and (5) both sexes showed a significant increase in the use of long-calls, yelps, and mews in offspring-oriented contexts.
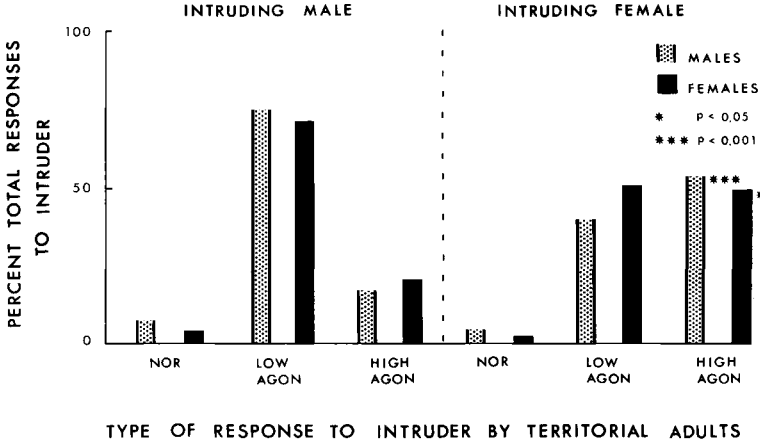
Fig. 11. Type of response (NOR = no obvious response, low-level agonistic, or high-level agonistic) directed at intruding males and females by defending adults. Results of Chi-square tests of comparisons (*) of the distribution of responses directed at intruders by males (317 responses) and females (114 responses) are indicated.

Agonistic behavior is an important investment for adults during the breeding season, due to the potential risk of injury during high-level agonistic interactions. Although attacks and fights are relatively rare, some adults do sustain eye and wing injuries during such encounters (pers. obs.). When compared with their mates, males consistently displayed higher frequencies of agonistic behavior, were more likely to exhibit high-level agonistic behavior towards non-neighboring intruders and female neighbors, generally exhibited an aggressive response to agonistic interactions between their mates and other adults, and were always dominant over their mates during interpair, agonistic interactions. Pierotti's (1981) observations of female Western Gulls attempting to relieve their mates on the nest in response to the landing of an intruder concurs with our post-hatch data concerning similar situations involving *L. marinus* pairs. This phenomenon may actually represent a "manipulation" on the part of the female for further investment by the male. In fact, increased aggressiveness on the part of male gulls may extend throughout the year, as Monaghan (1980) observed that male Herring Gulls were dominant over females and juveniles during feeding interactions in winter months. The relative risk to territory holders of engaging in agonistic interactions with normally more aggressive males may be reflected in the fact that intruding males generally elicited low-level responses from neighboring de-

fenders of either sex, while female intruders were more likely to stimulate high-level responses. The increased frequency of agonistic acts, as well as vocalizations given in agonistic contexts, by both sexes during the post-hatch period was probably associated with movements of chicks within the natal territory, the presence and movements of chicks (and corresponding movements of adults) on neighboring territories, the relative increase in the number of adult overflights related to foraging trips to feed chicks, and/or the increased investment adults have in older offspring. Previously reported post-hatch increases in territory size in Glaucous-winged Gulls (*L. glaucescens*) (Hunt and Hunt 1976), Herring Gulls (Burger 1980), and Great Black-backed Gulls (Butler and Janes-Butler 1982) are also probably related to increased offspring mobility.

Any explanation of sexual and seasonal differences in vocalizations (and their associated behavior patterns) necessitates some interpretation of their functional significance. This is sometimes difficult, because gull displays and vocalizations may have multiple, context-dependent messages and meanings (Beer 1975, 1980), and it is not always possible to determine context definitively. Choking, mewing, yelping, and long-calling occurred in a variety of contexts over the course of the breeding cycle. Greater pre-hatch frequencies of male mewing and choking (in mate-oriented contexts) may

PERCENT RESPONSE TO AGONISTIC INTERACTIONS INVOLVING MATES

PRE-HATCH

POST-HATCH

* P < 0.05
† P < 0.05
†† P < 0.01

NOR   AGON   NOR   AGON
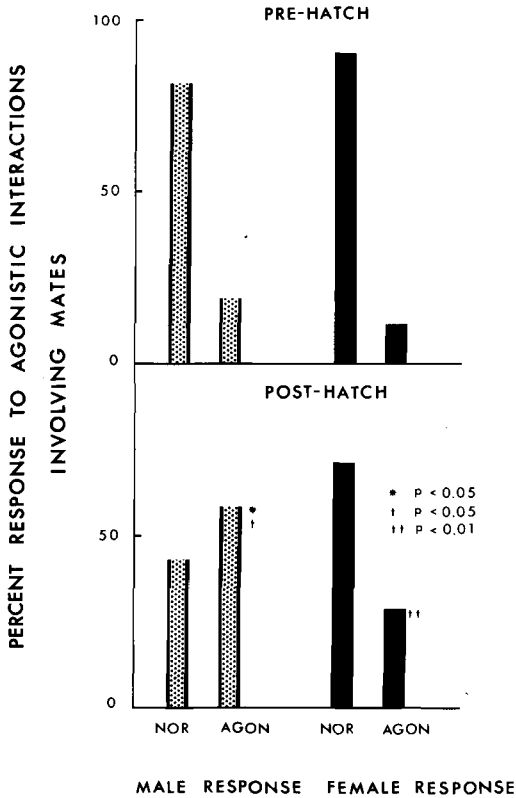
MALE RESPONSE   FEMALE RESPONSE

Fig. 12. Type of response (no obvious response = NOR or agonistic response) of adult males (42 responses) and females (108 responses) to agonistic interactions involving their mates. Results of Chi-square tests for both intersexual comparisons (*) and intrasexual comparisons between the pre- and post-hatch periods (†) are indicated.

this context. Although the significance of consistent sexual differences in yelping and long-calling during both the pre- and post-hatch periods remains unclear, the use of the latter in terms of advertisement and individual identification (Beer 1975, 1980), as well as the possible function of the yelp in this context, should not be overlooked. Stout's (1975; Stout et al. 1969) observations that the yelp of Glaucous-winged Gulls followed the termination of agonistic interactions are not inconsistent with this suggested function.

Gakkering and yeowing in Great Black-backed Gulls both appeared to function as alert/alarm vocalizations. Gakkering occurred frequently in agonistic contexts. It was also observed, however, when a human intruder approached the colony. Adults generally yeowed in response to high-level agonistic interactions nearby or when a chick wandered into the vicinity of a neighboring adult. This vocalization also was given in response to human intrusions into the colony, however, and during rare overflights of Ravens (*Corvus corax*). Both vocalizations appeared to be highly socially facilitated and often resulted in alerting large portions of the colony. The typical chick's response to these calls was to walk quickly out of sight into dense vegetation on the territory. We suggest that the post-hatch increase in frequence of yeowing was related to the increased vulnerability of mobile offspring to both conspecific aggression and predation.

Head-tossing and its accompanying vocalization have typically been ascribed the function of food-begging in female gulls during courtship (Tinbergen 1959, 1960). Smith (1980) has recently suggested that this type of behavior is actually an investment "demand" on the part of the females of some monogamous species. In *L. marinus* adults, males typically fed females during the pre-egg period, but both members of the pair exhibited head-tossing during the initial phases of courtship-feeding sequences. The behavior persisted in both sexes throughout the incubation period (even though courtship-feeding did not) and was most frequently observed when one adult joined its mate on the territory. Following chick hatching, the frequency of male head-tossing declined significantly, but females generally displayed this behavior during chick-feeding by the male. Continued female head-tossing following chick hatching may represent further

have been related to increased time investment by females in incubation and corresponding increased nest-relief attempts by males. The post-hatch increases in frequency of both mewing and yelping by both sexes were probably related to a major shift from agonistic and mate-related encounters to parent-offspring interactions. Both vocalizations (often given in combination) appeared in function to attract and/or locate chicks before feeding, when a chick was separated from the adult(s) in dense vegetation, when a chick had wandered out of its natal territory, or when a chick was in the vicinity of a neighboring adult. Evans (1980) has suggested that parent-chick recognition of individually distinctive mew calls in Ring-billed Gulls is reinforced through feeding, and the same may be true of the yelp of *L. marinus* in

"manipulation" of males that facilitates close approach of their mates to the site of chick feedings. Males did not generally react aggressively to approaching females that displayed head-tossing, although males often rapidly reconsumed food packages under these circumstances. Females were jabbed at or attacked by their mates only when they attempted to consume the food regurgitated for chicks. Females that obtained food in this manner were often observed feeding chicks themselves within an hour.

Trivers (1972) defined parental investment as "any investment by the parent in an individual offspring that increases the offspring's chance of surviving (and hence reproductive success) at the cost of the parent's ability to invest in other offspring." In this regard, much of the behavior displayed by an adult during the incubation and chick phases of the reproductive cycle (other than those that promote adult survival) may be considered investment in offspring. Trivers hypothesized that females (due to the larger size of their gametes) already have a greater investment in their offspring at fertilization and therefore should be willing further to invest more energy than males in parental care. Gladstone (1979), however, has questioned the actual "cost" of female gamete production relative to male energy expenditures and risks with regard to such activities as territorial defense. In fact, recent studies of the breeding biology of Northern Gannets (*Morus bassanus*; Montevecchi and Porter 1980) and Black Skimmers (*Rynchops niger*; Burger 1981b) have stated that male parental investment may equal or actually exceed that of females. Care must be taken, however, in designating behavioral acts related to reproductive effort as either parental investment or mating effort. For example, male territorial defense before clutch completion may aid in avoidance of cuckoldry, and agonistic behavior during this period would be considered primarily mating effort.

Moreover, interpretations of the relative investments of males and females in their offspring must be formulated cautiously because of the difficulty of equating such factors as the cost of gamete production, time spent in territorial attendance and incubation, the energy and risks involved in agonistic behavior, and future benefits accrued from territorial defense by site-tenacious species. Due both to the facts

that data in the present analysis were collected after clutch completion and that territorial defense appears to be related to chick survival (Butler and Janes-Butler 1982), we considered agonistic behavior of Great Black-backed Gulls in this study to be primarily parental investment. Although *L. marinus* females did invest statistically more time than males in territorial attendance (67% and 59%, respectively) and incubation (57% and 43%, respectively), these differences were small, and the activities involved were relatively risk-free. In contrast, males appeared to maximize their parental effort by investing significantly more in agonistic behavior than did females during both the pre- and post-hatch periods. In the absence of sexual differences in other types of parental care (e.g. post-hatch attendance, brooding, chick-feeding, etc.), the results of the present study strongly suggest that parental investment by male Great Black-backed Gulls may equal that of females. Pierotti (1981) observed a similar investment pattern in Western Gulls, but further investigation will be necessary to confirm whether this is typical for larids in general.

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