MATE AND NESTLING DESERTION IN COLONIAL LITTLE EGRETS

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ABSTRACT.—I observed 25 Little Egret (*Egretta garzetta*) nests during the nestling period. Eleven (44%) were deserted by the female parent, one (4%) by the male, and three (12%) by both parents. Deserters of both sexes left nests soon after single parent care became feasible ($\bar{x} = 22 \pm 4$ days after hatching, ca. 40% of the time from hatching to the independence of young). Small broods were deserted significantly more frequently than large ones. No chicks died after uniparental desertion. Deserters reacquired courtship coloration on their lores and repeatedly visited particular sites away from their nests before desertion, which suggests that they paired with new mates *before* leaving their primary nests. During biparental care periods, I found no sexual difference in feeding frequency, though males attended their young longer than females in the daytime. The tendency for female egrets to become ready to remate earlier than males may be because they invest less prezygotic effort in second breeding attempts than males. Males have to establish new territories and guard their new mates against extrapair copulations, although male-biased operational sex ratio also might favor female desertion.
Received 22 September 1988, accepted 16 December 1988.

BIPARENTAL care has typically been regarded as a manifestation of cooperative behavior, but recent discussions have emphasized the potential for evolutionary conflict between the sexes (Trivers 1972, Chase 1980, Davies and Houston 1986, Winkler 1987). Biparental care and "apparent" monogamy (*sensu* Gowaty 1983) are prevalent in birds, presumably because their external eggs and undeveloped chicks require substantial parental care before independence and both males and females can care for offspring (Lack 1968, Oring 1982). However, ". . . it is clear that monogamy is not *a* mating system, but a diverse array of reproductive strategies" (Mock 1985). Monogamy commonly involves extrapair copulation (Ford 1983, McKinney et al. 1984), occasional or facultative polygyny (Ford 1983), and female-female associations (Conover 1984a) within the same population. Desertion is another general variation on monogamy: either parent may try to reduce its share of parental care at the expense of its mate, while still ensuring the brood is reared successfully (Trivers 1972, Maynard Smith 1977, Ridley 1978, Winkler 1987).

Mate desertion can be defined as the termination of care by one (uniparental desertion) or both parents (biparental desertion) of the offspring in a breeding attempt before the offspring are capable of independent living. Desertion by males, which may result in polygyny, occurs occasionally among birds, but desertion by females (potential polyandry or multi-clutch systems) is far less common (Jenni 1974; Ridley 1978; Oring 1982, 1986). This sexual difference in mate desertion is more extreme in mammals where there are few maternal desertions (Kleiman 1977), but is occasionally reversed in amphibians (Ridley 1978, Wells 1981) and especially in fishes, where paternal care is more prevalent than maternal care (Blumer 1979, Baylis 1981, Gross and Shine 1981, Kuwamura 1987, and references therein).

Recent studies have documented facultative uniparental desertion by both sexes (ambisexual desertion: Beissinger 1986) within populations of biparental birds and fishes (Dowsett-Lemaire 1979; Solheim 1983; Blumer 1985, 1986). For the Snail Kite (*Rostrhamus sociabilis*), estimates of relative reproductive investments have allowed prediction of which parent will desert (Beissinger 1987a, b; Beissinger and Snyder 1987). Among colonial wading birds, where biparental care appears to be favored strongly and breeding patterns are relatively homogeneous (Wittenberger and Hunt 1985), uniparental desertion has not been reported. Biparental desertion, however, was recently suggested as a response to reduced brood size (Mock and Parker 1986).

I focused on the division of parental duties, mate and nestling desertion, and nestling mor-

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tality in the Little Egret (*Egretta garzetta*). About one-half of 25 nests were deserted. Strong circumstantial evidence suggests that the deserters remated elsewhere in the same colony before they had abandoned their primary nests. I discuss possible reasons that desertion was so common, that some individuals deserted whereas others did not, and that females deserted more frequently than males (comparing the desertion option with the alternative of renesting with the same mate).

METHODS

Study species.—The Little Egret is a colonial wading bird of the Old World tropical and temperate regions. Little Egrets feed on fish, insects, amphibians, and aquatic crustaceans in a wide variety of habitats (Hafner et al. 1982, Fujioka unpubl. data).

The color of the lores changes dramatically to magenta before pair formation (called *courtship coloration* in this paper, see below), then it fades gradually to the noncourting appearance of straw yellow by the time the last egg is laid (see Blaker 1969b, Cramp and Simmons 1977). Both parents share nesting duties after egg laying, but brood reduction due to starvation is common (Inoue 1981, 1985). Parents take ca. 1 month to hatch eggs after completion of pair-formation. Nestlings require full-time brooding for only 2-3 weeks after hatching (Inoue 1980) and probably become independent at 8–9 weeks of age (Fujioka unpubl. data). Thus, a complete breeding cycle (from pair formation to the independence of all chicks) requires at least 3 months. The frequency of parental feedings seems to decrease after the middle of the nestling period, as reported for the Cattle Egret (*Bubulcus ibis*; Fujioka 1985).

Study sites.—I studied two breeding colonies in two years: the Suzuka colony from early May to early September 1982 and the Hamajima colony from early March to early July 1986. The Suzuka colony was located 15 km north of Tsu City, Mie Prefecture, Japan (34°50'N, 135°35'E), on a small island in a pond surrounded mostly by rice fields, and was destroyed in 1985. Five ardeid species, including ca. 200 Little Egret pairs, nested in an area of ca. 0.28 ha in 2-m to 7-m tall pine forest. Additional information on this colony can be found in Fujioka and Yamagishi (1981).

The Hamajima colony is located 65 km south of the Suzuka colony (34°18'N, 136°46'E). This colony probably started in ca. 1976, when live sardines were first stocked in fish reserves around the site. Little Egrets foraged in the reserves and along natural coasts at a nearby bay. Five or six ardeid species, including ca. 300 Little Egret pairs, nested in an area of ca. 0.75 ha in a 4-m to 15-m tall coastal forest. The forest consists mainly of Japanese black pines (*Pinus thunbergii*) and an evergreen oak (*Quercus philyraeoides*).

Observation and analysis.—One 5.3-m high blind was built at the edge of the colony during the breeding season in 1982. In 1986 two elevated blinds (7.0 m and 5.3 m), which afforded wide views over the tree crowns, were built on the top of the hill before the breeding season with above-ground tunnels (see Shugart et al. 1981) for access to the blinds with little disturbance.

In 1982 newly hatched chicks in focal nests (see below) were marked individually with felt-tip pens during daily nest inspections, and later marked with feather dye and colored leg bands. Body mass and tarsus length were measured every 2-5 days until the chicks were ca. 14 days old. In 1986 contents of focal nests (see below) were checked almost every day from the blinds. To reduce disturbance, chicks were measured only once and banded when they were about 12 days old; then they were assigned hatching order according to relative tarsus lengths. Because of large size asymmetries among siblings (see Inoue 1981, 1985), chicks that hatched third or later (often dead before measuring) were distinguishable from the blinds without marking. Brood size was defined as the number of surviving chicks at the time of desertion or day 22 (see Results for mean age of deserted broods) for nests not deserted. Broods of 1-2 chicks were designated as "small"; those of ≥ 3 chicks were termed "large."

Individual adult Little Egrets were easily distinguished by idiosyncratic color patterns on their legs where yellow-black boundaries were variable, clear, and stable. In 1986 I used a paint gun (Fitch and Shugart 1983) to mark 15 male and 5 female parents of focal nests without capturing them. This made it possible to easily recognize those individuals, even when they were away from their nests. Because the sexes are identical, gender of adults was determined by courtship displays, egg laying, or positions during copulations.

Behavioral observation usually began just after sunrise and continued until ca. 30 min after sunset. In both years, I recorded *nest visitation rate* (parental visits per hour that included food deliveries) and *nest attendance* (percentage of time a parent was at the nest or within ca. 5 m of the nest) every 2-6 days for each nest. The color of lores, which was divided into five grades (straw yellow, powder white, pink, rose, and magenta; after Palmer 1962), also was recorded at the daily observation. The latter three grades were considered *courtship coloration.* In 1986 I counted the unmated males that established courtship territories within ca. 20 m of the blinds and the unmated females with courtship coloration that approached the unmated males in a manner unique to courting females (see Blaker 1969a). Up to 11 nests within a single range of view were observed unaided or with binoculars simultaneously from the blinds. Data were recorded on a portable computer (see Hensler et al. 1986) and in notebooks.

TABLE 1. Parental care and desertion patterns in relation to sex and brood size in Little Egrets at the Suzuka (1982) and Hamajima (1986) colonies in Japan.

Nesting status[a] (male-female)	Year		Brood size[b]		Season[c]		Difference in care days[d]
	1982	1986	1-2	3-4	Early	Late	
Desert-Desert	—	3	3	—	2	1	0.7 ± 1.2
Desert-Color	—	1	1	—	1	1	9.0
Color-Desert	—	4	2	2	3	1	14.6 ± 4.0
Stay-Desert	1	6	4	3	1	5	15.0 ± 5.2
Stay-Color	—	5	—	5	4	1	
Stay-Stay	3	2	1	4	—	2	
Total	4	21	11	14	11	10	

[a] Desert = desertion; Color = courtship coloration but no desertion; Stay = neither courtship coloration nor desertion. There were no instances of the other three possible combinations (i.e. Color-Color, Color-Stay, and Desert-Stay).

[b] Both years combined.

[c] Early = before or on 15 May; Late = after 15 May. Data from 1986 only.

[d] The mean difference (male minus female in days ± SD) in duration of parental care between the partners.

The chronology for each brood was counted from the day the first chick hatched (day 0). Because parental activities changed with time, I divided the nestling period into two stages for further analyses. The *first half* was defined as the period from day 0 until one parent deserted or, for nests that were not deserted, the mean desertion period of 22 days (see Results). The *second half* was defined as the period after desertion (i.e. uniparental period) or after the mean desertion day (including days after the chicks reached flying age). Data from the two stages were not combined. In comparisons between deserted nests and nests that were not deserted or between the sexes in all nests, only data from the first half were used.

A parent was defined as having deserted its mate and young if it showed courtship coloration and no longer fed the primary brood of dependent young. One exceptional female, which first stopped and then (20 days later) provided care, was not counted as a deserter. Those nests that were not deserted (i.e. in which both parents continued to feed young throughout the observation period) were called *biparental care nests.* Furthermore, parents that did not desert the nests, but showed courtship coloration at more than one observation were considered to be attempting to renest. The *duration of parental care* was calculated for each nesting adult as the period from hatching (brood age 0) to the end of the observation for each nondeserter, and to the midpont between the last feeding day and the first nonfeeding day for deserters. This definition makes the difference between deserters and nondeserters small. Even though I did not record parental behavior quantitatively, all nondeserters continued to feed chicks until at least day 40 in all but the last four nests in 1986.

I restricted all analyses to nests that were monitored for at least one month post-hatching or until both parents deserted the young. Data from observation periods of <2 h were excluded. The resulting sample was 4 nests in 1982, observed on 26 days (totaling 371 h and 429 nest-h) between 4 June and 6 August, and 21 nests in 1986, observed on 33 days (333 h and 1,408 nest-h) between 17 April and 2 July. In addition, 1-6 of the 1986 focal nests were monitored with a portable video camera system on 17 days (183 h and 249 nest-h). Because parental activities of one individual may depend on those of its partner, the measurement of pairs (or nests), not individuals, was regarded as an independent variable except when comparisons were made within pairs. When no significant differences were found between years/colonies, the data were combined. In comparisons between categories, I excluded data based on total observations of <20 h/nest (or per individual). When samples did not always have equal variances and the sample sizes were small, I used nonparametric statistical tests (Sokal and Rohlf 1981). All mean values are given with one standard deviation (±SD).

RESULTS

Occurrence of desertion.—I observed a total of 15 mate desertions by 18 parents: 1 female desertion (25.0%) among 4 nests at Suzuka in 1982 and 10 female (47.6%), 3 biparental (14.3%), and 1 (4.8%) male desertion among 21 nests at Hamajima in 1986 (Table 1). In 2 of the 3 biparental desertions, the male deserted the brood on the same day as their mates and 2 days after female desertions, the males deserted the brood on the plete nest failure. At only one 1986 nest, the male parent deserted the brood, while the female continued to feed the brood. Overall, females deserted the young and mates significantly more frequently than males (14 females vs. 4 males in 25 pairs; Fisher's exact test, $P = 0.007$).

Additional "remating attempts," inferred from the coloration of lores, comprised 10 of 50 total parents (Table 1). In the last two nests in 1986, neither parent regained courtship coloration. The proportion of parents that showed courtship coloration, including deserters, was significantly greater at Hamajima (64.3% of 42) than at Suzuka (12.5% of 8; $P = 0.015$, Fisher's exact test). Females reacquired courtship coloration significantly more often than males (20 vs. 8 in 25 pairs; $G = 10.196$, $P < 0.005$). At 4 nests deserted by females, the males also reassumed courtship coloration and flew to sites different from where their mates had flown; the males continued to feed their first broods. In 1 of 10 biparental care nests, the female reacquired courtship coloration, disappeared from her first nest for 20 days (days 17.5–38), but then resumed feeding her original chicks.

Uniparental desertion or first desertion in biparental desertions usually occurred ca. 3 weeks after first hatching ($\bar{x}$ = day 21.9 ± 4.1, range = 16.5–29.5, $n = 15$). Small broods were deserted more frequently than large broods (Table 1; $P = 0.012$, Fisher's exact test).

Because the mean date of first hatching in 4 nests of 1982 (14 June ± 12 days) differed significantly from that in 21 nests of 1986 (17 May ± 11 days; Mann-Whitney test, $U = 82$, $P < 0.01$), I examined the effect of season for 1986 only (Table 1). Probability of desertion was not related to hatching date: 7 of 11 early nests (the first chick hatched on or before the median hatching date of 15 May) were deserted and desertion occurred at 7 of the other 10 nests ($P = 1.0$, Fisher's exact test). Similarly, there was no difference in the mean hatching date between deserters (14 May ± 13 days, $n = 17$) and nondeserters (19 May ± 9 days, $n = 25$; Mann-Whitney test, $U = 263.5$). However, the mean hatching date of parents that developed courtship coloration (14 May ± 11 days, $n = 27$) was significantly earlier than that of the others (22 May ± 10 days, $n = 15$; Mann-Whitney test, $U = 299.5$, $P < 0.05$).

Deserting parents and other birds that had courtship coloration were observed repeatedly visiting particular colony areas. Because of the restricted view from the blinds, renesting by deserters could not be confirmed. However, such females were often seen intently watching courting males. Similarly, such males were seen defending their courtship territories. In the lone case of male desertion, the male probably renested with his original mate, which had also exhibited courtship coloration. Both flew repeatedly to the same restricted area unusually close (ca. 15 m) to their previous nest, where they repeatedly performed "greeting ceremonies" (Blaker 1969b). Renesting by one male (a nondeserter) was confirmed. The new nest, about 90 m from the previous one, contained three eggs on day 30 of the first brood. He continued to provide solo care to the original brood of two young, which had been deserted by the female. The fate of the second nest was not monitored.

Parental care.—Male Little Egrets attended chicks for slightly longer periods than females in the daytime, both in deserted and biparental care nests, but the frequency of nest visits did not differ between the sexes in either deserted or biparental care nests (Table 2). The mean duration of male parental care was about a week longer than that of females (Table 2). This estimate is conservative because most nests were not monitored through the end of parental care.

Brood size had no effect on either nest attendance or visitation rates, among either deserted nests or all focal nests (Table 3). Also, no difference was found in the timing of desertion as a function of brood size. Individuals that subsequently deserted their broods visited nests at the same rate as their mates (0.17 ± 0.04 visits/h vs. 0.18 ± 0.05 visits/h, $n = 12$ pairs, Wilcoxon signed-ranks test, $T = 27.5$).

Prior to uniparental desertions, future deserters tended to spend less time at their nests (47.3 ± 10.6%, $n = 12$) than their mates (58.2 ± 9.3%: Wilcoxon signed-ranks test, $T = 2$, $P < 0.01$). However, because all but one of these deserters were females, this result may be autocorrelated with the basic gender-bias (see Table 2). Likelihood of desertion did not appear to be related to particularly high levels of parental care: total attendance rates during the first half of the nestling period were similar for nests eventually deserted (54.0 ± 8.4%, $n = 15$) compared with those not deserted (55.6 ± 4.5%, $n = 10$: Mann-Whitney test, $U = 79.5$). These two classes of nests also received comparable visitation rates from parents (0.17 ± 0.04 visits/h vs. 0.18 ± 0.05 visits/h, $U = 93.5$). Furthermore, males whose mates had deserted them did not differ from males in biparental care nests with respect to both attendance rates (15.0 ± 12.8%, $n = 8$ vs. 11.2 ± 10.4%, $n = 6$; Mann-Whitney test, U

TABLE 2. Comparisons of parental care between sexes in Little Egrets at the Suzuka (1982) and Hamajima (1986) colonies in Japan ($\bar{x} \pm$ SD).

Desertion categories[a]	Male	Female	n	Wilcoxon test[b] T	Wilcoxon test[b] P
Nest attendance (%)					
Deserted (1st-half)	58.5 ± 8.1	49.4 ± 11.1	15	8	<0.01
Biparental (1st-half)	59.4 ± 6.3	51.8 ± 7.5	10	9	<0.05
Biparental (2nd-half)	11.2 ± 10.4	6.6 ± 7.0	6	0	<0.05
Nest visits/h					
Deserted (1st-half)	0.17 ± 0.05	0.17 ± 0.04	15	40	NS
Biparental (1st-half)	0.18 ± 0.05	0.18 ± 0.07	10	20.5	NS
Biparental (2nd-half)	0.33 ± 0.06	0.24 ± 0.09	6	2	NS
Duration of care[c]	34.7 ± 8.6	28.1 ± 8.6	25	5	<0.01

[a] The "1st half" of the nestling period is the duration from the first hatching to the time one parent deserted the brood for deserted nests or to the mean desertion day (21.9) for biparental care nests. The "2nd half" is all days thereafter.

[b] Wilcoxon's signed-ranks test. ANOVAs yielded the same results for all but nest attendance in biparental care nests during the second half.

[c] The period from the first hatching to the desertion or the end of observation (see Methods for details).

= 29) and visitation rates (0.32 ± 0.08 visits/h vs. 0.33 ± 0.06 visits/h, $U = 27.5$).

Brood reduction.—Brood reduction could be related to parental desertion in three ways: (1) chicks may die as a result of desertion, (2) risk of chick starvation may reduce the incentive for parents to desert their chicks, and (3) parents may desert their brood as a result of brood reduction (because of the brood's lower reproductive value).

Initial brood sizes (number of chicks hatching) were 4.3 ± 1.0 in 4 nests of 1982 and 3.5 ± 1.6 in 21 nests of 1986. Three of 17 chicks in 1982 and 18 of 74 chicks in 1986 died during the first half of the nestling period. All three in 1982 were siblings of a nest where the female parent eventually deserted two remaining nestlings. The chicks died during days of heavy rain, apparently because of starvation. In 1986, three died from the observer's disturbance; one fell from its nest and disappeared; another died of totally unknown causes; and the other 13 mortalities (72%) were apparently due to starvation (Table 4). Of 7 chicks that died after being measured, 3 fourth-hatched chicks weighed only 34.6 ± 3.9% of their first-hatched sibling in each nest, significantly lighter on a relative scale than the 6 fourth-hatched chicks that survived (56.9 ± 13.3%; Mann-Whitney test, $U = 21$, $P < 0.01$). The other 3 fifth-hatched chicks also were severely underweight (averaging 25.2 ± 5.5%). Comparative data on survival chicks were not available because all fifth-hatched chicks died.

Brood reduction did not result in a higher

TABLE 3. Comparisons of parental care in relation to brood size in Little Egrets at the Suzuka (1982) and Hamajima (1986) colonies ($\bar{x} \pm$ SD, number of nests in parentheses). No U value was significant.

Desertion categories[a]	Small broods[b]	Large broods[b]	U[c]
Nest attendance (%)			
Deserted (1st-half)	53.4 ± 10.1 (10)	55.0 ± 4.1 (5)	26
Deserted (2nd-half)	16.0 ± 18.1 (4)	14.1 ± 7.3 (4)	9
Pooled (1st-half)	53.4 ± 9.6 (11)	55.6 ± 4.3 (14)	83
Nest visits/h			
Desertion (1st-half)	0.17 ± 0.04 (10)	0.17 ± 0.03 (5)	27
Desertion (2nd-half)	0.31 ± 0.12 (4)	0.34 ± 0.04 (4)	12
Pooled (1st-half)	0.17 ± 0.04 (11)	0.17 ± 0.04 (14)	84
Desertion timing[d]	21.4 ± 4.1 (10)	22.9 ± 4.3 (5)	32

[a] Same as Table 2. Comparison was not made between biparental care nests alone because there was only one small brood.

[b] Small broods had 1 or 2 chicks; large broods 3 or more chicks.

[c] Mann-Whitney U-test.

[d] Days from the first hatching to the uniparental desertion (see Methods).

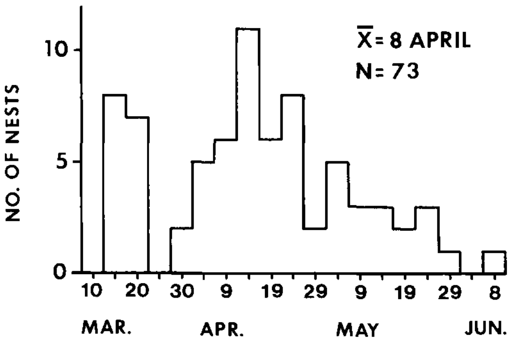

Fig. 1. The distribution of laying dates of first eggs by Little Egrets at the Hamajima colony in Japan (1986).

frequency of desertion. One or both parents deserted 6 (46.2%) of 13 nests where brood reduction had occurred; 8 (72.7%) of 11 nests were deserted where all chicks survived ($P = 0.240$, Fisher's exact test). This may be because brood reduction occurred more frequently in large broods, where desertion was less frequent (see above) than in small broods.

During the second half of the nestling period, 4 chicks died as a direct result of biparental desertion. However, no chicks died either after uniparental desertion or at biparental care nests. Two males each reared broods of 4 chicks uniparentally, the maximum number that survived in Hamajima broods.

Breeding season and sex ratio.—At Hamajima, laying occurred over at least 88 days, from 15 March to 10 June (Fig. 1). Most early nests were destroyed by strong winds in late March, creating two peaks in laying. Because several nestlings were observed in September, laying probably continued until the end of June.

The number of courting males and courting females (the operational sex ratio, *sensu* Emlen and Oring 1977) varied with time (Fig. 2). Courting females tended to outnumber courting males for the first month of the study. Thereafter, unmated males were almost always more common than females. No unmated males established a territory within the study area after 27 May, but many males still displayed in more distant parts of the colony.

DISCUSSION

Variation in the occurrence of desertion.—It is not clear why desertion was common at the study colonies, especially at Hamajima. Desertion may

TABLE 4. Brood reduction in relation to initial brood size in Little Egrets at the Hamajima colony (1986). The numbers of nests are given.

Nestlings dead (n)	Initial brood size[a] 1	2	3	4	5	6	Total
0	2	5	1	—	—	—	8
1	—	1	—	3	5	—	9
2	—	—	—	1	1	1	3
	Mortality (%)						
	0	8.3	0	31.3	23.3	33.3	21.7

[a] One brood of 4 chicks was excluded because 3 died after nest disturbance.

have been overlooked in previous studies of colonial wading birds because of the difficulties associated with individually marking these large birds and because full biparental care was presumed obligate. Three species-specific features, along with environmental factors, probably affect the frequency of desertion in a population.

The effect of uniparental care on reproductive success relative to those of biparental care varies from species to species even among monogamous animals (Wittenberger and Tilson 1980). It depends on offspring demand for care (a function of brood size and brood age) and, in a particular season or area, on variation in food availability. Beissinger and Snyder (1987) found that no desertion occurred in Snail Kites during drought years, whereas uniparental desertion occurred at nearly every nest during favorable years.

The breeding season must be long enough for the parents (or at least for the deserters) to renest (Beissinger 1987a). I found that there were unmated individuals of both sexes during a relatively long period (Fig. 2). Similarly, asynchronous breeding offers a greater chance for renesting (Maynard Smith 1977). Egrets have relatively long periods during which eggs are laid (e.g. 67–78 days for Cattle Egrets, Blaker 1969a; at least 88 days in this study, Fig. 1) compared with other gregarious birds (e.g. 67% of Bank Swallow [*Riparia riparia*] nests may hatch during a single 6-day period, Emlen and Demong 1975).

Another important factor may be the amount of resources available to breeding pairs. If there are some resources for renesting in the territories, intrasexual conflict could physically prevent renesting with new mates by either sex (e.g. Freed 1987). A parallel argument has been

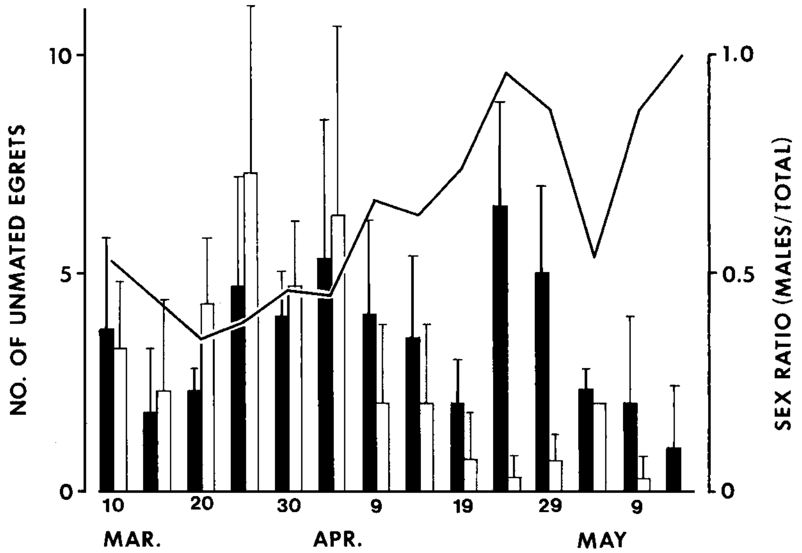

Fig. 2. The number of courting Little Egret males (black bars) and females (white bars) with 1 SD, and the operational sex ratio (*sensu* Emlen and Oring 1977: line) around the blind at the Hamajima colony in Japan (1986). The maximum number of courting egrets per day that were individually distinguished was averaged across 5 days (3 or more observation days per 5-day stage). The last courting bachelor was seen in the observation area on 27 May and the last courting female on 11 May, but several apparently unmated egrets were seen later in other areas of the colony.

made for male polyterritorialism (Slagsvold and Lifjeld 1988).

Decision making.—Several facts suggest that Little Egret deserters may have engaged in courtship (or pair formation) activities before deserting. Deserters showed a resurgence of courtship coloration while still taking care of the young. These color changes may accurately predict remating potential. Male egrets that lose their mates are known to remate soon after they reacquire courtship coloration (Fujioka 1986). Those egrets that showed courtship coloration, including future deserters, flew repeatedly to particular areas in the colony while tending a nest. Finally, six females and four males showed courtship coloration but did not desert. Some of them might have tried to remate but failed.

Beissinger (1987b) reported reduced parental care in Snail Kite deserters before desertion and suggested that such birds might be testing their mates' commitment and capability of caring for the young without help. I found no reduced care, probably because I sampled nest visitation, a less sensitive measure than amount of food delivered. When such estimates were made in 1982, however, the female parents did reduce their contributions before deserting at one Little Egret nest and one Cattle Egret nest (Fujioka unpubl. data).

Potential deserters probably look for new mates while reducing care to current broods, then desert only if they acquire a new mate and if their young seem likely to be reared by the current partner. In such a protracted decision-making process, the individual can adopt or give up an alternative tactic according to relatively accurate prediction (i.e. few mistakes). In this sense, the process contrasts with situations in which an individual must forsake alternatives in order to adopt a tactic that may be more profitable *on average*.

Although many factors are involved in desertion patterns (Winkler 1987), decision making depends fundamentally on two basic variables: the probability of renesting and the impact that uniparental care of the current brood will have on reproductive success. In general, desertion should be favored when

$$V_1 + pV_2 > (1 + p')V_2 \qquad (1)$$

where V_1 and V_2 are the expected reproductive success of uniparental and biparental care, respectively, and p and p' are the chances of renesting after desertion and nondesertion, respectively (Maynard Smith 1977, 1982). In addition, there are the probabilities, q, that the partner will desert the brood first, and r that the partner also will desert, thus not provide the necessary uniparental care. Taking these variables in account, Equation 1 becomes

$$(1 - r)V_1 + pV_2 > qV_1 + (1 - q)V_2 + p'V_2. \quad (2)$$

The assumptions in this formula are that average reproductive success does not change with time during the season, and that chicks cannot survive without care from at least one parent.

If a parent has already found a new mate (i.e. $p = 1$) and "knows" that the present brood can be raised fully by its former partner alone (i.e. $V_1 = V_2$), then desertion is favored whenever

$$p' < 1 - r \text{ or } r < 1 - p', \quad (3)$$

that is, whenever the probability of renesting with the same mate or risk of biparental desertion is low. For Little Egrets I calculated r as 0.12 (3 of 25 pairs) and p' as 0.04 (1 of 25 pairs, assuming that the sole case of "male desertion" resulted in renesting by the same pair). Therefore, desertion would be favored after the critical point of biparental care (see below) whenever a new mate has been found.

In the care periods of many biparental species, there may be a critical point after which uniparental care becomes feasible (i.e. after the phase when offspring require the highest levels of parental care). I found deserters provided care long enough to ensure chick survival, but for only about 40% of the normal nestling period. Although several chicks died of starvation during the early nestling period with biparental care, no chicks died after uniparental desertion. At least one deserted male egret managed to take care of the young and still renest with another female. Male terns (*Sterna hirundo*) can raise chicks alone after mate loss in the middle of the nestling period (Nisbet et al. 1978), whereas mate loss before the critical timing may result in nest failure in gulls (*Larus* spp.) (Conover 1984b) or infanticide in egrets (Fujioka 1986). With mate removal experiments, Sasvári (1986) demonstrated that lone Great Tit (*Parus major*) and Blue Tit (*P. caeruleus*) parents were unable to rear chicks less than about a week old although they raised older chicks.

Brood size can influence the decision to desert in two ways. First, uniparental feeding may be sufficient for small but not for large broods. Second, the expected brood size in the next breeding attempt may differ from that of the present brood. Therefore, small broods may be deserted more frequently than large broods (this study, S. R. Beissinger MS, Lazarus and Inglis 1986, Winkler 1987 for theoretical models). Beissinger and Snyder (1987) also reported that single chick broods tended to be deserted earlier than larger broods. Similarly, Mock and Parker (1986) found high mortality among singleton Great Egrets (*Casmerodius albus*) and Great Blue Herons (*Ardea herodias*), suggesting a high biparental desertion rate.

Sex-skewed investment.—Female Little Egrets deserted mates and nestlings more often than males. Equation 3 explains neither this fact nor why parents did not simply renest with the same partners ("clutch overlap," Burley 1980).

In colonial birds, the reproductive effort may be larger in males than in females simply because foraging and mate guarding are incompatible activities (Beissinger 1987a). Male colonial birds have to defend courtship territories, produce gametes, guard mates against extrapair copulations, and provide food to females, while the primary cost for females is egg production (Hunt 1980, Røskaft 1983, Røskaft et al. 1983, Røskaft and Slagsvold 1985, Beissinger 1987a). This early disparity does not reverse because parental duties after laying or hatching are shared equally (or slightly male-biased) between both parents (e.g. Hunt 1980, Montevecchi and Porter 1980, Burger 1981, Leffelaar and Robertson 1986, Beissinger 1987b, this study). Unlike males nesting in dispersed territories, which can have more than one nest in the same territory, colonial males must repeat all these investments in order to remate. Thus, regardless of the amount each parent has invested in the present offspring, renesting costs may be lower for colonial females. This asymmetry may make it possible for females to be ready to remate earlier than males. There is no reason that females should wait for mates to be ready to renest.

A deserting female needs a new partner (indeed, a monogamous one) because biparental care is obligate during the early breeding stage in colonial birds. Over an entire population, therefore, males theoretically have an equal chance to remate unless the sex ratio of potential breeders is skewed toward males. In fact, some Little Egret males deserted or remated after desertion by their mates. Little Egret females often fight among themselves over access to courting males when the operational sex ratio is skewed toward females (Fujioka 1987). The observed sexual difference in desertion may be due in part to the temporarily male-biased operational sex ratio (Fig. 2).

ACKNOWLEDGMENTS

I thank S. Yamagishi for advice and encouragement throughout this study as part of my Ph.D. dissertation at the Department of Biology, Osaka City University. This paper was completed while I was a visiting researcher at the Department of Zoology, University of Oklahoma, and the Department of Psychology, University of Washington. I am particularly grateful to D. W. Mock. I am also grateful to M. I. Beilharz, R. Kishimoto, M. Kohda, J. Quinn, K. Ueda, E. Urano, and especially S. R. Beissinger, T. C. Lamey, D. W. Mock, J. A. Rodgers Jr., P. L. Schwagmeyer, and an anonymous referee for many useful comments on various versions of the manuscript. This study could not have been completed without the long-term assistance with the field observation by N. Yabe and assistance in other aspects of the fieldwork by M. A. Fitch, D. Hashiguchi, Y. Higuchi, M. Hotta, Y. Inoue, R. Kishimoto, and S. Komeda. Instruction in computer programs and statistical analyses was from T. C. Lamey and H. Momose. I received unpublished data from S. R. Beissinger and Y. Inoue. Many references were searched and managed by a cooperative database system, the Data Bank of Ornithological Literature, Japan. This research was supported in part by a Grant-in-Aid for Encouragement of Young Scientists (No. 60790034) from the Japanese Ministry of Education, Science and Culture, a Fellowship for Young Scientists and a Fellowship for Research Abroad by the Japan Society for the Promotion of Science.

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