# REPRODUCTIVE PERFORMANCE OF FEMALE-FEMALE PAIRS AND POLYGYNOUS TRIOS OF RING-BILLED GULLS

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ABSTRACT.—We studied female-female pairs of Ring-billed Gulls (*Larus delawarensis*) on Granite Island, northern Lake Superior, during the breeding seasons of 1979 and 1980. In 1979 the colony consisted of approximately 2,400 nesting pairs, with a total of 99 nests containing 5–7 eggs (superclutches). In 1980 the colony had increased in size to 2,600 nests and contained a total of 71 superclutches. We discuss the difficulty of distinguishing nests in which superclutches have been laid by female-female pairs from single-cup nests used by polygynous groups or from nests receiving dump eggs. Nests containing superclutches were larger than those containing normal-sized clutches. They were not differentially located by substrate, nest density, or location within the colony. Nearest-neighbour distance was also similar for the two clutch types.

Eggs laid in superclutches were slightly smaller than those from normal-sized clutches (1–4 eggs) but did not differ in shape. Significantly more eggs from superclutches rolled from the nest or were destroyed or abandoned than from normal-sized clutches. The proportion of nests that hatched at least one chick did not differ significantly between the two clutch types. Hatching success for superclutches was 34% in 1979 and 30% in 1980, whereas for normal-sized clutches it was 77% in 1979 and 61% in 1980. Chicks from superclutches had a higher rate of mortality during the week following hatching than did chicks from normal-sized clutches. Chicks from the former hatched at significantly lighter weights than did those from the latter during both years of study, but their weights did not differ after the first week posthatch. Tarsal and culmen measurements followed a similar pattern to that of weight. Chicks from normal-sized clutches had a significantly higher fledging success than did those from superclutches. The reproductive success of four polygynous groups is also reported. *Received 13 October 1982, accepted 21 February 1983.*

MONOGAMY and polygamy are considered normal mating systems in birds. Various environmental and social factors are believed to advance one system or the other (Emlen and Oring 1977, Wilson 1980). Until recently, homosexual mating behavior was documented only from captive and semicaptive individuals (Collias and Jahn 1959; Slater, cited in Jefferies 1967; Sauer 1972; Starkey 1972; Dilger, cited in Hunt 1980; Hand in press). Hunt and Hunt's (1977) discovery of female-female pairs of Western Gulls (*Larus occidentalis*) incubating superclutches added an avian mating system that had been previously undocumented in the wild to the list of normal mating systems. The subsequent discovery of such pairs of California Gulls (*L. californicus;* Conover et al. 1979), Ring-billed Gulls (*L. delawarensis*) (Conover et al. 1979, Ryder and Somppi 1977), and Herring Gulls (*L. argentatus;* Fitch 1979) has led to speculation about the origin(s) and biological significance of female-female pairs and has stimulated a reevaluation of common beliefs about mate selection, sex roles, pair bonding, and sex ratios (Ryder 1978a, 1979; Hunt 1980; Hunt et al. 1980; Wingfield et al. 1980; Oring 1982).

Researchers have reported a significantly lower rate of egg fertility (Hunt and Hunt 1977, Conover et al. 1979, Ryder and Somppi 1979) and reduced hatching success (Hunt and Hunt 1977, Ryder and Somppi 1979) in female-female pairs as compared to heterosexual pairs. Mate fidelity between members of female-female pairs has also been reported (Hunt and Hunt 1977, Kovacs and Ryder 1981). To date, however, there have been no detailed reports of the breeding biology of such pairs. In this paper we report the reproductive success of members of female-female pairs of Ring-billed Gulls and compare it to that of conspecific heterosexual

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pairs. We also report the success experienced by four polygynous trios.

## Materials and Methods

This study was conducted at the Ring-billed Gull colony on Granite Island (48°41′N, 88°29′W) in Black Bay, northern Lake Superior (Ryder 1975). In 1979 we arrived on Granite Island on 14 May but left again until 20 May because of the prevalence of snow and ice and the low number of clutches (approximately 30) that had been initiated. In 1980 we arrived 6 May; only scrapes and one-egg clutches were present. We postponed extensive colony searches and marking of clutches until 11 May to avoid disturbance during the early establishment of territories.

Clutches on the exposed summit area of the island (see Ryder 1975), chosen because of its relative accessibility, were marked with stakes if they contained two or more eggs and with a numbered wooden block if they contained one egg. New clutches were marked daily with numbered blocks to determine when clutches were initiated and to obtain a sample of clutches with known initiation dates. During 1979, 70 nests containing 3 or 4 eggs were randomly chosen as a control group from among previously marked nests that had been initiated during the peak period of clutch initiation. The success of the control group could thus be compared with the success of superclutches (nests containing 5+ eggs). In 1980, control nests were chosen according to clutch initiation dates only. We monitored 25 early, 59 peak, and 26 late nests containing 1–4 eggs to avoid any bias that may have occurred by restricting the 1979 control sample only to peak nests containing 3 or 4 eggs. Control clutches and the resultant chicks were handled in the same manner and with the same frequency as superclutches and their chicks to avoid bias from disturbance.

We searched daily throughout the colony for superclutches during both years in order to determine the frequency, location in the colony, and date of completion of superclutches. A numbered wooden block was placed beside each superclutch for identification, and the site was mapped for future reference. Nests with a common rim were marked in the same manner, as Shugart and Southern (1977) and Shugart (1980) found these "figure 8" arrangements diagnostic of polygynous groups. All superclutches and double-cupped nests were monitored.

In 1980, nearest-neighbor distance (the distance from the center of a nest to the center of the nearest nest), nest density (the number of neighbors within a 2-m radius) and length (greatest diameter of the nest) and width (90° from length) were measured for control and superclutches. We also noted substrate to determine whether or not actual nest sites differed between the two clutch types. These data were collected, as time permitted, during the third week after peak clutch initiation, when few clutches were being initiated and nest construction had been completed for most nests.

To allow identification of eggs after they had rolled out of or were destroyed near the nest, eggs in both control and superclutch nests were marked on the blunt end with a non-toxic black felt pen in 1979 and with brown-colored nail enamel in 1980. Nail enamel was used during the second year because it is durable and reduced disturbance caused by repeated visits to re-mark eggs with felt pens. We measured the maximum length and breadth of each egg with vernier calipers (±0.01 cm) and determined egg volume (Ryder 1975) and shape (Coulson 1963). To check fertility, we opened in the field the eggs that had rolled out of the nest or had been abandoned and inspected them for developing embryos or for lacunae in the blastodisc, indicating infertility (Hunt and Hunt 1977).

We recorded the fates of eggs by visiting the nests daily and keeping histories until several days after hatching began. After this time we visited nests without pipping eggs once every 2 days to reduce potential chick mortality from investigator disturbance. Chicks were marked within 24 h of hatching by placing a numbered aluminum fingerling fish tag through one web of the right foot; they were weighed with a hand-held Pesola 50-g spring scale. During 1980 culmen and tarsus length (Baldwin et al. 1931) also were measured with vernier calipers (±0.01 cm). Using appropriately larger Pesola scales as the chicks grew, we recorded these growth parameters every few days. Fledging success (Dexheimer and Southern 1974) was calculated following the method of Ryder and Carroll (1978): missing chicks were classified as dead or fledged according to the age at which they were last seen, corresponding to the proportion of tagged chicks found dead at that age out of the total number dead. Separate estimates were made each year for each clutch type.

In 1979, 11 gulls incubating normal clutches and 58 incubating superclutches were trapped using a drop trap (Mills and Ryder 1979). During 1980, 45 attendants at normal-sized clutches and 69 superclutch attendants were trapped, as well as two pairs of females incubating normal-sized clutches. Measurements of gonys and gape (Baldwin et al. 1931) were taken with vernier calipers (±0.01 cm). Sex was determined using discriminant function analysis (Ryder 1978b). Five birds attending superclutches were collected and their gonads examined to verify the measurement results.

A colony census was conducted each year, on 7 June 1979 and on 30–31 May 1980. These dates represent similar points in the nesting cycle of the 2 y. Observation hides were used to study the behavior of heterosexual versus female-female pair behavior throughout the breeding season. Results will be published in a companion paper (Kovacs in prep.).

TABLE 1. Characteristics of nests containing control clutches and superclutches of Ring-billed Gulls, Granite Island.

| | Control[a] | Super[a] |
|---|---|---|
| Length (cm) | 28.3 ± 7.4 (99) | 31.3 ± 13.2 (56) |
| Width (cm) | 25.5 ± 5.0 (99) | 28.3 ± 5.0 (56) |
| Nest density[b] | 4.4 ± 1.9 (98) | 4.5 ± 2.5 (46) |
| Nearest-neighbor distance (cm) | 83.6 ± 31.8 (97) | 79.8 ± 40.0 (46) |
| Substrate | | |
| Rock | 24 (24.7)[c] | 10 (21.3)[c] |
| Dirt | 73 (75.3)[c] | 37 (78.7)[c] |

[a] Mean ± SD (*n*).
[b] Number of neighbors within a 2-m radius.
[c] Numbers in parentheses are percentages of totals.

## RESULTS

In 1979 the Ring-billed Gull colony on Granite Island consisted of approximately 2,400 nesting pairs, with 99 nests containing 5-7 eggs. In 1980, the colony had increased in size to 2,600 nests and contained a total of 71 superclutches. Two known female-female pairs laid completed clutches containing 3 and 4 eggs, respectively, in 1980.

Egg laying began before our arrival on Granite Island on 14 May 1979 and continued through 9 July. The peak period of clutch initiation occurred 20–22 May. Clutch completion dates were used for comparative purposes between control and superclutches, because the latter were not recognizable until a fifth egg was laid. Nine five-egg clutches were present on 20 May. The majority of superclutches (75/99, 76%) that occurred during 1979 were completed within a week of the modal completion date (24 May) for normal-sized clutches in the summit area. In 1980 egg laying had begun before we arrived on 6 May. The peak period of clutch initiation occurred 11–13 May. The first five-egg clutch of 1980 was recorded 12 May. Again, the majority of superclutches (57/71, 80%) was completed within a week of the modal completion date (15 May) for normal-sized clutches in the summit area.

TABLE 2. Comparison of length, breadth, volume, and shape index of eggs from control clutches and superclutches of Ring-billed Gulls, Granite Island.

| | Control[a] | Super[a] | *t*-value |
|---|---|---|---|
| Length (mm) | | | |
| 1979 | 59.1 ± 2.3 | 58.9 ± 2.6 | 0.92, $P > 0.05$ |
| 1980 | 59.0 ± 2.4 | 58.6 ± 2.6 | 1.98, $P < 0.05$ |
| Breadth (mm) | | | |
| 1979 | 42.2 ± 1.3 | 41.8 ± 1.1 | 4.41, $P < 0.05$ |
| 1980 | 42.0 ± 1.3 | 41.9 ± 1.4 | 0.98, $P > 0.05$ |
| Volume ($mm^3$)[b] | | | |
| 1979 | 51.6 ± 3.8 | 50.3 ± 3.8 | 3.81, $P < 0.05$ |
| 1980 | 51.0 ± 4.2 | 50.4 ± 4.3 | 1.71, $P > 0.05$ |
| Shape[c] | | | |
| 1979 | 71.5 ± 3.3 | 71.1 ± 3.4 | 1.70, $P > 0.05$ |
| 1980 | 71.3 ± 3.0 | 71.7 ± 3.5 | 1.24, $P > 0.05$ |
| Sample size[d] | | | |
| 1979 | 193 | 466 | |
| 1980 | 279 | 355 | |

[a] Mean ± SD.
[b] 0.489 × breadth$^2$ × length (Ryder 1975).
[c] 100 × breadth of the egg divided by its length (Coulson 1963).
[d] Sample sizes are not indicative of the total number of eggs laid. Some eggs were destroyed or were "missing" before they had been measured.

Nearest-neighbor distance did not differ between control and superclutches ($t = 0.56$, $P > 0.05$), nor did nest density ($t = 0.05$, $P > 0.05$; Table 1). Similarly, there was no difference in nest location by substrate ($\chi^2 = 0.2$, df = 1, $P > 0.05$; Table 1). Nests containing superclutches were significantly longer ($t = 3.3$, $P < 0.05$) and wider ($t = 3.1$, $P < 0.05$) than control nests (Table 1). Superclutches were distributed throughout the colony, with no apparent pattern of clumping.

Length, width, and volume of eggs from control clutches were greater than those of eggs from superclutches during both years of study (Table 2). Only width and volume during 1979 and length during 1980 differed significantly. The shape of eggs from the two clutch types did not differ (Table 2).

The fates of unhatched eggs from the two clutch types are compared in Table 3. There was a significant difference in the frequency of occurrence of fate categories between control and superclutches (1979: $\chi^2 = 22.5$, df = 8, $P < 0.05$; 1980: $\chi^2 = 43.6$, df = 7, $P < 0.05$). The dif-

TABLE 3. Fates of eggs from control clutches and superclutches of Ring-billed Gulls, Granite Island.

| | 1979[a] | | 1980[a] | |
|---|---|---|---|---|
| Fate | Control | Super | Control | Super[b] |
| Cracked | 9 (4.6) | 36 (6.8) | 9 (2.9) | 16 (4.1) |
| Missing | 18 (9.2) | 117 (22.0) | 82 (26.5) | 106 (26.8) |
| Rolled out of nest | 10 (5.1) | 116 (21.9) | 5 (1.6) | 58 (14.4) |
| Dead embryo | 0 | 2 (0.4) | 0 | 1 (0.3) |
| Destroyed | 0 | 34 (6.4) | 14 (4.5) | 54 (13.7) |
| Dead during pipping | 1 (0.4) | 16 (3.0) | 2 (0.7) | 9 (2.3) |
| Buried in nest | 0 | 7 (1.3) | 0 | 5 (1.3) |
| Abandoned | 7 (3.6) | 25 (4.7) | 10 (3.2) | 30 (7.6) |
| Storm | 0 | 1 (0.2) | 0 | 0 |

[a] Numbers in parentheses are percentages of the total number of eggs.
[b] Includes one 3-egg and one 4-egg clutch attended by female-female pairs.

ferences in the frequency of rolled, destroyed, and abandoned eggs account for most of the variation. In addition to having higher frequencies of these shared causes of egg loss, superclutches also had eggs buried in the nest cup.

Fertility rates of superclutches were significantly lower than those of control clutches (1979: $\chi^2 = 6.8$, df = 1, $P < 0.05$; 1980: $\chi^2 = 26.9$, df = 1, $P < 0.05$; Table 4). Because of egg losses and our uncertainty in distinguishing infertile eggs from those in which the embryo died at a very young age, there is a large undetermined fertility category.

The number of nests that hatched at least one egg (Table 5) did not differ significantly between superclutches and control clutches (1979: $\chi^2 = 3.08$, df = 1, $P > 0.05$; 1980: $\chi^2 = 0.01$, df = 1, $P > 0.05$). Hatching success, the number of eggs that hatched/eggs laid (Table 5), did differ significantly (1979: $\chi^2 = 110.0$, df = 1, $P < 0.05$; 1980: $\chi^2 = 69.8$, df = 1, $P < 0.05$). In 1979, superclutches hatched an average of 1.8 ± 1.1 (range 0–5) chicks per nest, while control clutches hatched an average of 2.2 ± 1.1 (range 0–4) chicks per nest. In 1980, superclutches hatched 1.6 ± 1.3 (range 0–5) chicks per nest as opposed to 1.7 ± 1.3 (range 0–4) in control clutches.

Most chick deaths occurred during the week following hatching. This trend was most pronounced for chicks from superclutches (Fig. 1). The cause of death in most cases was pecking on the head by adult gulls (chicks from control clutches 69%, superclutches 50%). Exposure and crushing in the nest were more prevalent in superclutches than in control clutches: 35% versus 12%. In 20% of control chick deaths and 15% of superclutch chick deaths the cause of death could not be determined.

In both years, chicks from control clutches hatched at significantly higher weights than did those from superclutches [1979: 41.1 ± 3.6 g ($\bar{x}$ ± SD) and 30.0 ± 5.0 g, $t = 2.61$, df = 244, $P < 0.05$; 1980: 41.8 ± 2.8 g and 38.2 ± 4.2 g, $t = 1.38$, df = 236, $P < 0.05$]. In 1979 this dichotomy was not present for 2-day-old chicks but was again seen for those 3 days old. During 1980 chicks from superclutches remained significantly lighter than chicks from control clutches until 4 days of age. From this time on their weights did not differ significantly (Figs. 2 and 3). Regression lines of the $\log_e$ transformed weight data illustrate the lower hatching weight and faster growth rate of chicks from superclutches. The correlation coefficient between the transformed weight data and age was

TABLE 4. Fertility of eggs from control clutches and superclutches of Ring-billed Gulls, Granite Island.

| | Normal[a] | Super[a] |
|---|---|---|
| Fertile | | |
| 1979 | 152 (99.3) | 228 (94.2) |
| 1980 | 197 (99.5) | 182 (86.7) |
| Infertile | | |
| 1979 | 1 (0.7) | 14 (5.8) |
| 1980 | 1 (0.5) | 28 (13.3) |
| Undetermined | | |
| 1979 | 43 | 289 |
| 1980 | 111 | 185 |
| Total number of eggs | | |
| 1979 | 196 | 531 |
| 1980 | 309 | 395[b] |

[a] Numbers in parentheses are percentages of the total number of eggs known to be fertile or infertile.
[b] Includes one 3-egg and one 4-egg clutch attended by female-female pairs.

TABLE 5. Percentage of nests that hatched at least one egg and percentage hatching success of control clutches and superclutches of Ring-billed Gulls, Granite Island.

| | Percentage of nests that hatched at least one chick[a] | Percentage hatching success[b] |
|---|---|---|
| 1979 | | |
| Control | 87.1 (61) | 77.0 (151) |
| Super | 69.7 (69) | 34.4 (177) |
| 1980 | | |
| Control | 67.3 (74) | 60.5 (187) |
| Super | 69.4 (50) | 29.6 (117)[c] |

[a] Numbers in parentheses are the number of nests that hatched at least 1 chick.
[b] Numbers in parentheses are the number of eggs that hatched.
[c] Includes one 3-egg and one 4-egg clutch attended by female-female pairs.

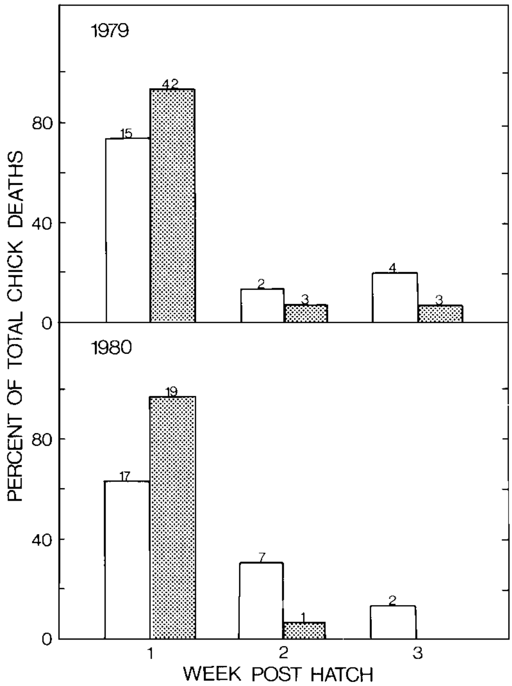


Fig. 1. Age at death by weeks from hatching to 21 days of age for Ring-billed Gull chicks from control clutches and superclutches, Granite Island. Clear bars = control clutches, stippled bars = superclutches.

0.96 in all cases except for the control sample from 1979, which was 0.95.

Tarsus measurements followed the same pattern as did weight, chicks from control clutches being larger until day 3 (Fig. 4). Culmen measurements did not differ significantly between chicks from the two clutch types at any age. Mean values were consistently lower, however, for chicks from superclutches during the first 7 days after hatching (Fig. 4).

Chicks from control clutches had a significantly higher fledging success than did those from superclutches (estimated fledging success: 1979: $\chi^2 = 37.0$, df = 1, $P < 0.05$; 1980: $\chi^2 = 45.1$, df = 1, $P < 0.05$; Fig. 5).

The sex of birds trapped on superclutches and control clutches is shown in Table 6. Of the 5 superclutch attendants collected, 3 were males and 2 were females, as their measurements had indicated. In the observation areas where all attendants of the 25 superclutches visible from the hides were known, 21 (84%) superclutches were attended by female-female pairs, and the other 4 (16%) were attended by polygynous trios. Two of these four polygynous groups had figure-8 nest arrangements; the other two used single cups. The hatching successes of the four polygynous groups were 0/6, 1/6, 3/5, 3/5 eggs, respectively. None of the chicks survived to the age of 7 days.

## DISCUSSION

It is difficult to determine the exact number of female-female pairs or polygynous groups in a gull colony. Hunt and Hunt (1977), Conover et al. (1979), and this study all report low incidences of female-female pairs incubating normal-sized clutches. Ryder and Somppi (1979) discussed the difficulty of distinguishing superclutches produced by homosexual pairs from nests that had received eggs by dumping. It is also difficult to separate female-female pairs from polygynous groups unless all of the attendants are trapped. Conover et al. (1979) found no double-cupped nests but did trap three females and one male using a single nest cup. In one instance during our study, a female-female pair's nest became double-cupped because the females built the nest cup around two eggs that had rolled out of the nest. This might have been the case for the birds described by Southern (1978). Despite these difficulties, the number of superclutches is probably a reasonable approximation of the incidence of female-female pairing in Ring-billed Gulls, as indicated by their frequency on these clutches in observation areas where most

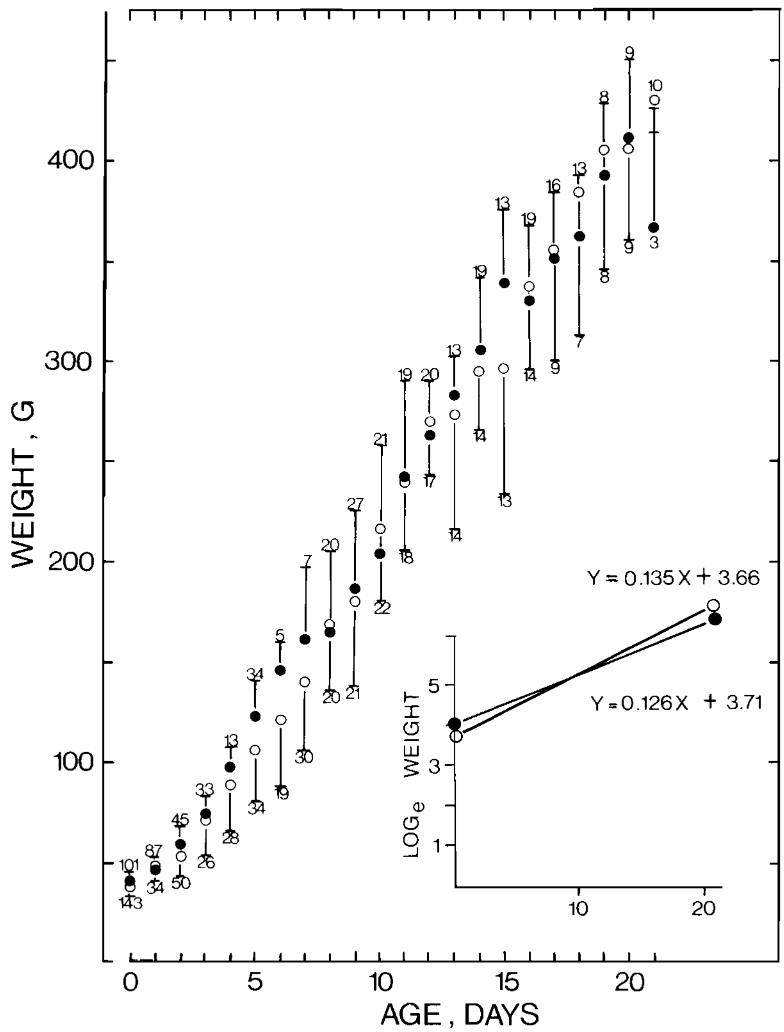


Fig. 2. Mean weights of chicks hatching from control clutches (+SD) and superclutches (−SD) of Ring-billed Gulls from the day of hatch (Day 0) until 21 days of age, Granite Island, 1979. Numbers above or below SD bars are sample sizes. The inserted graph is a plot of the $\log_e$ transformed weight data against age ● = control clutches, ○ = superclutches.

attendants were trapped, banded and dyed, and extensively observed.

Somppi (1978) and Ryder and Somppi (1979) reported that all their superclutches attended by female-female pairs were initiated early in the season. During this study, the completion of superclutches had a temporal distribution similar to that of normal-sized clutches. The peak for the control sample was more pronounced, however, because this sample was restricted to a single area in the colony, whereas superclutches were distributed throughout the colony.

Inter-nest distances of control nests during 1980 were similar to those reported by Somppi (1978; 83 versus 86 cm) and greater than those found by Vermeer (1970; 60 cm) for Ring-billed Gulls. Vermeer (1970) measured the nest from rim to rim, rather than from center to center as we and Somppi (1978) did. The similarity of nearest-neighbor distance and nest density of control clutches to those of superclutches, as

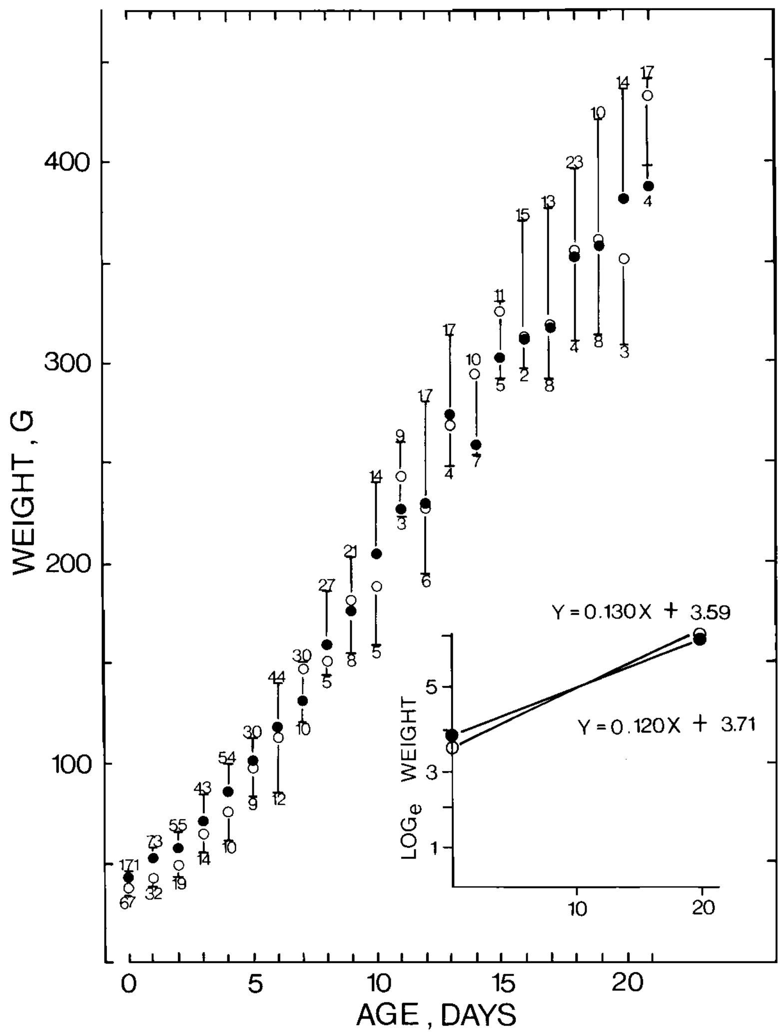


Fig. 3. Mean weights of chicks hatching from control clutches (+SD) and superclutches (−SD) of Ring-billed Gulls from the day of hatch (Day 0) until 21 days of age, Granite Island, 1980. Numbers above or below SD bars are sample sizes. The inserted graph is a plot of the $\log_e$ transformed weight data against age. ● = control clutches, ○ = superclutches.

well as the distribution of superclutches throughout the Granite Island colony, indicates that the female-female pairs were not located in suboptimal habitat, where younger and less-experienced or poorer quality birds frequently locate (Coulson 1968, Dexheimer and Southern 1974, Ryder 1975).

The slightly smaller size of eggs laid by the females of female-female pairs of Ring-bills may be due to the lack of courtship feeding of these birds (Kovacs 1982), as Hunt and Hunt (1977) suggested was the case for similar pairs of Western Gulls. The correlation between the nutritional status of females at the time of laying and its effects on egg size, however, are somewhat controversial. Some researchers consider that the nutritional status of the female and the food available to her at the time of laying are factors that contribute to egg size (Lemmetyinen 1973, Scott 1973, Murton et al. 1974, Mills 1979, Schreiber et al. 1979, Coulson et al. 1982). Others have shown or intimated

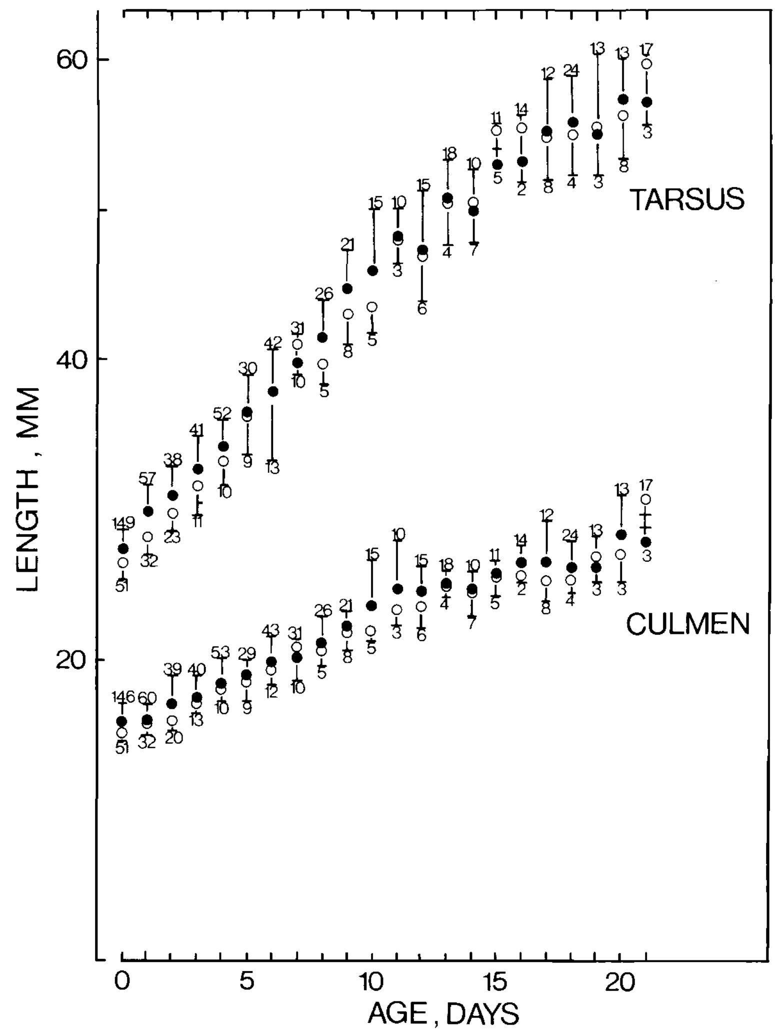


Fig. 4. Tarsus and culmen growth of chicks hatching from control clutches (+SD) and superclutches (−SD) of Ring-billed Gulls from the day of hatch (Day 0) until 21 days of age, Granite Island, 1980. ● = control clutches, ○ = superclutches.

that these factors are not important (Coulson et al. 1969, Bryant 1975, Parsons 1975). Some researchers have stated that the male's efficiency in courtship feeding may influence egg size by supplying energy to the female during egg formation (Cullen and Ashmole 1963; Lack 1966, 1968; Mills 1973; Nisbet 1973; Davis 1975). The lack of any difference in egg shape between eggs from control and superclutches may reflect the similar age and reproductive condition (Romanoff and Romanoff 1949) of birds attending the two clutch types (Kovacs 1982).

Ryder and Somppi (1979) and Coulter (1973) also reported a higher incidence of eggs rolling from the nest cup or being buried in the nest in superclutches than in normal-sized clutches. This may be because of excessive crowding in the nest. The frequency of abandoned eggs was higher in superclutches than in control clutches, perhaps because of the greater potential for the eggs in a superclutch to vary in the length of incubation time. If females of a pair laid asynchronously, the chicks of the first clutch would hatch before the chicks of the second clutch were fully developed.

Hunt and Hunt (1977) reported that in West-

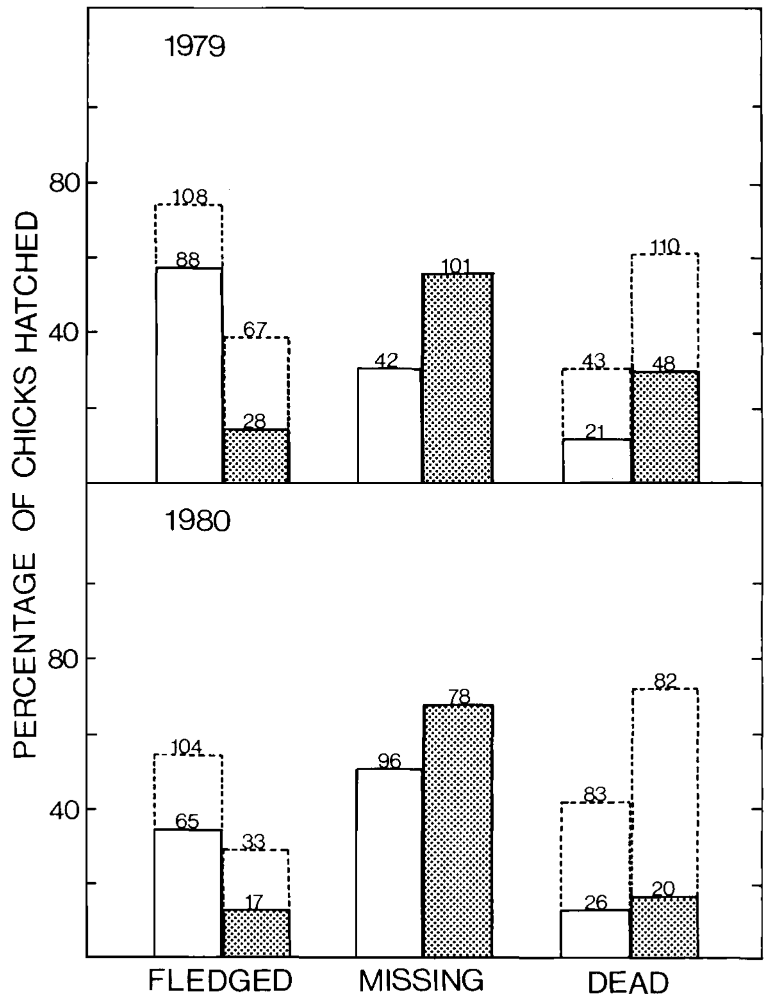


Fig. 5. Fates of chicks hatching from control clutches and superclutches of Ring-billed Gulls on Granite Island. Dotted lines = calculated estimates (Ryder and Carroll 1978, see text for explanation), clear bars = control clutches, stippled bars = superclutches.

ern Gulls 81.5% of the eggs in three-egg clutches and 13% of the eggs in superclutches were fertile. Conover et al. (1979) reported that 65–70% of the eggs in 5- and 6-egg clutches of Ring-billed Gulls showed development and that 9 of 10 eggs examined from 4-egg clutches of California Gulls proved fertile. Ryder and Somppi (1979) reported a 66% fertility rate for Ring-billed Gull superclutches. The fertility rates for superclutches in the present study were higher than those reported by Conover et al. (1979) and Ryder and Somppi (1979). We were not able to determine fertility for all of the eggs in 1979 or 1980, however, because many disappeared and others were addled when checked, so our results may be biased.

Ryder and Somppi (1979) reported a 21% maximum hatching success for superclutches laid by female-female pairs of Ring-bills. Other authors working with larids have also found that clutches containing more than three eggs had lower hatching success (Schreiber 1970, Hunt and Hunt 1973, Ryder 1975, Ryder and Ryder 1981). The significant difference in hatching success between control clutches in 1979 and 1980 was due mainly to the difference in sampling methodology previously described. Different levels of predation during

TABLE 6. Sex [determined by measurement (Ryder 1978a)] of trapped birds incubating normal-sized clutches and superclutches of Ring-billed Gulls, Granite Island.

| | Normal[a] | Super[a] |
|---|---|---|
| 1979 | | |
| Males | 7 (63.6) | 2 (2.6)[b] |
| Females | 4 (36.4) | 56 (96.4) |
| 1980 | | |
| Males | 17 (34.7) | 8 (11.6) |
| Females | 32 (65.3)[c] | 61 (88.4) |

[a] Numbers in parentheses are percentages of the total number of birds caught each year.
[b] One male was known to be a member of a polygynous group.
[c] Four of these females were members of (2) female-female pairs.

each year may also have had some influence on success. Common Crows (*Corvus brachyrhynchos*) were seen taking eggs infrequently during 1979 and 1980, and an otter (*Lutra canadensis*) was also seen swimming near the island at dusk both years, although it was never seen in the colony. During 1980, a Snowy Owl (*Nyctea scandiaca*) caused losses in some areas of the colony, taking one or two adults a night for several weeks, which resulted in the eggs being eaten or abandoned. In addition, egg predation by Herring and Ring-billed gulls was more prevalent in 1980.

We found, as have others working with Ring-billed Gulls (Vermeer 1970, Somppi 1978, Ryder and Ryder 1981), that well over 50% of the total chick mortality occurred during the first week post-hatch. The smaller territory held by some female-female pairs (Kovacs 1982) may have influenced the number of chicks killed by neighbors (Hunt and Hunt 1976, Butler and Trivelpiece 1981) and hence may account for some of the difference in mortality between the two clutch types. The higher frequency of chicks being crushed to death in superclutch nests than in control-clutch nests may indicate that female-female pair members may have more difficulty making the transition from incubation to brood rearing. If the females of a pair laid asynchronously, the female that laid last may not have sufficiently high prolactin and low progesterone levels to change smoothly from incubation to brood-rearing activities. The slightly smaller egg size and hatching weight also may have influenced survivability (Parsons 1970, Lundberg and Väisänen 1979).

There have been few published reports on the growth rates of Ring-billed Gull chicks. Kirkham and Morris (1979) referred to the growth of seven early and six late chicks but did not provide actual weight data. Available data (Vermeer 1970, present study) suggest that Ring-billed Gulls have a standard sigmoid growth curve as defined by Ricklefs (1968). The weights of chicks weighed after 20 days of age were substantially heavier than those reported by Vermeer (1970) for chicks of the same age. Although the hatching weight was lower for chicks in superclutches than for those in control clutches, there was no statistical difference in fledging weight. The faster rate of growth experienced by chicks from superclutches could be a result of the reduced brood size. Vermeer (1970) found that single-chick broods grew more quickly than did those containing two or three. The rate of growth of chicks from superclutches reflects the ability of the two female parents to provide sufficient food for their broods.

A wide range in fledging success has been reported in studies on Ring-billed Gulls (Emlen 1956, 22%; Vermeer 1970, 40%; Ryder and Ryder 1981, 55%). The fledging rates calculated here for control pairs during 1979 and 1980 were above average (40%) for Ring-billed Gulls. This may be due to different methods of calculating fledging success, as Emlen (1956) and Vermeer (1970) did not define their criteria. Seasonal variation might also be a factor.

Several hypotheses have been proposed regarding the origin(s) of female-female pairing in gulls (Ryder 1978a, Wingfield et al. 1980). Most infer a skewed sex ratio in favour of females. If female-female pairing is a response to an unequal sex ratio (Fry and Toone 1981), whatever its cause, female-female pairing raises from zero the probability that excess females will raise offspring (Hunt and Hunt 1977) and exemplifies the lability of larid mating systems.

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LITERATURE CITED

BALDWIN, S. P., H. C. OBERHOLSER, & L. G. WORLEY. 1931. Measurements of birds. Sci. Publ. Cleveland Mus. Nat. Hist. 2: 1-167.

BRYANT, D. M. 1975. Breeding biology of House Martins *Delichon urbica* in relation to insect abundance. Ibis 117: 180-216.

BUTLER, G. R., & W. TRIVELPIECE. 1981. Nest spacing, reproductive success and the behaviour of the Great Black-backed Gull (*Larus marinus*). Auk 98: 99-107.

COLLIAS, N. E., & L. R. JAHN. 1959. Social behaviour and breeding success in Canada Geese (*Branta canadensis*) confined under semi-natural conditions. Auk 76: 478-509.

CONOVER, M. R., D. E. MILLER, & G. L. HUNT, JR. 1979. Female-female pairs and other unusual reproductive associations in Ring-billed and California gulls. Auk 96: 6-9.

COULSON, J. C. 1963. Egg size and shape in the Kittiwake (*Rissa tridactyla*) and their use in estimating age composition of populations. Proc. Zool. Soc. London 140: 221-227.

———. 1968. Differences in the quality of birds nesting in the center and on the edges of a colony. Nature 217: 478-479.

———, G. R. POTTS, & J. HOROBIN. 1969. Variation in the eggs of the Shag, *Phalacrocorax aristoltelis*. Auk 86: 232-245.

———, N. DUNCAN, & C. THOMAS. 1982. Changes in the breeding biology of the Herring Gull (*Larus argentatus*) induced by reduction in the size and density of the colony. J. Anim. Ecol. 52: 739-756.

COULTER, M. C. 1973. Breeding biology of the Western Gull (*Larus occidentalis*). Unpublished M.Sc. thesis. Oxford, Oxford Univ.

CULLEN, J. M., & N. P. ASHMOLE. 1963. The Black Noddy *Anous tenuirostris* on Ascension Island. Part 2. Behaviour. Ibis 103: 423-446.

DAVIS, J. W. F. 1975. Age, egg-size and breeding success in the Herring Gull *Larus argentatus*. Ibis 117: 460-473.

DEXHEIMER, M., & W. E. SOUTHERN. 1974. Breeding success relative to nest location and density in Ring-billed Gull colonies. Wilson Bull. 86: 288-290.

EMLEN, J. T. 1956. Juvenile mortality in a Ring-billed Gull colony. Wilson Bull. 68: 232-258.

EMLEN, S. T., & L. W. ORING. 1977. Ecology, sexual selection, and the evolution of mating systems. Science 197: 215-223.

FITCH, M. 1979. Monogamy, polygamy and female-female pairs in Herring Gulls. Proc. Colonial Waterbird Group 3: 44-48.

FRY, M. D., & C. K. TOONE. 1981. DDT-induced feminization of gull embryos. Science 213: 922-924.

HAND, J. L. In press. Sociobiological implications of unusual sexual behaviors of gulls: the genotype/behavioral phenotype problem. Ethol. Sociobiol.

HUNT, G. L., JR. 1980. Mate selection and mating systems in seabirds. Pp. 113-151 *in* Behavior of marine animals, Vol. 4 (J. Burger, B. L. Olla, and H. E. Winn, Eds.). New York, Plenum Publishing Corp.

———, & M. W. Hunt. 1973. Clutch size, hatching success and eggshell-thinning in Western Gulls. Condor 75: 483-486.

———, & ———. 1976. Gull chick survival: the significance of growth rates, timing of breeding and territory size. Ecology 57: 62-75.

———, & ———. 1977. Female-female pairing in Western Gulls in southern California. Science 196: 1466-1467.

———, J. C. WINGFIELD, A. NEWMAN, & D. S. FARNER. 1980. Sex ratio of Western Gulls on Santa Barbara Island. Auk 67: 474-479.

JEFFERIES, D. 1967. The delay in ovulation produced by ppt-DDT and its possible significance in the field. Ibis 109: 266-272.

KIRKHAM, I. R., & R. D. MORRIS. 1979. Feeding ecology of Ring-billed Gull (*Larus delawarensis*) chicks. Can. J. Zool. 57: 1086-1090.

KOVACS, K. M. 1982. Behavior and reproductive success of female-female pairs of Ring-billed Gulls, Granite Island. Unpublished M.Sc. thesis. Thunder Bay, Ontario, Lakehead Univ.

———, & J. P. RYDER. 1981. Nest-site tenacity and mate fidelity in female-female pairs of Ring-billed Gulls. Auk 98: 625-627.

LACK, D. 1966. Population studies of birds. Oxford, Clarendon Press.

———. 1968. Ecological adaptations for breeding in birds. London, Chapman and Hall.

LEMMETYINEN, R. 1973. Breeding success in *Sterna pardisaea* Pontopp and *S. hirundo* L. in southern Finland. Ann. Zool. Fennica 10: 526-535.

LUNDBERG, C., & R. A. VÄISÄNEN. 1979. Selective correlation of egg-size with chick mortality in the Black-headed Gull (*Larus ridibundus*). Condor 81: 146-156.

MILLS, J. A. 1973. The influence of age and pair-bond on the breeding biology of the Red-billed Gull *Larus novaehollandiae scopulinus*. J. Anim. Ecol. 42: 147-162.

———. 1979. Factors affecting the egg size of Red-billed Gulls (*Larus novaehollandiae scopulinus*). Ibis 121: 53-67.

———, & J. P. RYDER. 1979. Trap for capturing shore and seabirds. Bird-Banding 50: 121-123.

MURTON, R. K., N. J. WESTWOOD, & A. J. ISAACS. 1974. Factors affecting egg weight, body weight and moult of the Woodpigeon *Columba palumbus*. Ibis 116: 52-73.

NISBET, I. C. T. 1973. Courtship-feeding, egg size and breeding success in Common Tern. Nature 241: 141-142.

ORING, L. W. 1982. Avian mating systems. Pp. 1-92 *in* Avian biology, Vol. 6 (D. S. Farner, J. R. King, and K. C. Parkes, Eds.). New York, Academic Press.

PARSONS, J. 1970. Relationship between egg size and posthatching chick mortality in the Herring Gull (*Larus argentatus*). Nature 228: 1221- 1222.

———. 1975. Seasonal variation in the breeding success of the Herring Gull: an experimental approach to pre-fledging success. J. Anim. Ecol. 44: 553-573.

RICKLEFS, R. E. 1968. Patterns of growth in birds. Ibis 110: 419- 451.

ROMANOFF, A. L., & A. J. ROMANOFF. 1949. The avian egg. New York, Wiley.

RYDER, J. P. 1975. Egg-laying, egg size and success in relation to immature-mature plumage of Ring-billed Gulls. Wilson Bull. 87: 534-542.

———. 1978a. Possible origins and adaptive value of female-female pairing in gulls. Proc. Colonial Waterbird Group 2: 138-145.

———. 1978b. Sexing Ring-billed Gulls externally. Bird-Banding 49: 218-222.

———. 1979. A preliminary investigation of the secondary sex ratio of Ring-billed Gulls on Granite Island (abstract only). Proc. 1979 Colonial Waterbird Group No. 256.

———, & T. R. CARROLL. 1978. Reproductive success of Herring Gulls on Granite Island, northern Lake Superior, 1975 and 1976. Can. Field-Natur. 92: 51-54.

———, & P. L. SOMPPI. 1979. Female-female pairing in Ring-billed Gulls. Auk 96: 1-5.

RYDER, P. L., & J. P. RYDER. 1981. Reprodutive performance of Ring-billed Gulls in relation to nest location. Condor 83: 57-60.

SAUER, E. G. F. 1972. Aberrant sexual behaviour of the South African Ostrich. Auk 89: 717-737.

SCHREIBER, E. A., R. W. SCHREIBER, & J. J. DINSMORE. 1979. Breeding biology of Laughing Gulls in Florida, part 1: nesting, egg and incubation parameters. Bird-Banding 50: 304-321.

SCHREIBER, R. W. 1970. Breeding biology of Western Gulls (*Larus occidentalis*) on San Nicolas Island, California, 1968. Condor 72: 133-150.

SCOTT, M. L. 1973. Nutrition in reproduction—direct effects and predictive functions. Pp. 46-59 *in* The breeding biology of birds (D. S. Farner, Ed.). Washington, D.C., Natl. Acad. Sci.

SHUGART, G. W. 1980. Frequency and distribution of polygyny in Great Lakes Herring Gulls in 1978. Condor 82: 426-429.

———, & W. E. SOUTHERN. 1977. Close nesting, a result of polygyny in Herring Gulls. Bird-Banding 48: 276-277.

SOMPPI, P. L. 1978. Reproductive performance of Ring-billed Gulls in relation to nest location. Unpublished M.Sc. thesis, Thunder Bay, Ontario, Lakehead Univ.

SOUTHERN, W. E. 1978. Ring-billed Gull pair with two nests. Wilson Bull. 90: 299-301.

STARKEY, E. E. 1972. A case of interspecific homosexuality in geese. Auk 89: 456-457.

VERMEER, K. 1970. Breeding biology of California and Ring-billed gulls: a study of ecological adaptation to inland habitat. Can. Wildl. Serv. Rept. 12.

WILSON, E. O. 1980. Sociobiology. Cambridge, Massachusetts, Belknap Press.

WINGFIELD, J. C., A. MARTIN, M. W. HUNT, G. L. HUNT, JR., & D. S. FARNER. 1980. Origin of homosexual pairing of female Western Gulls on Santa Barbara Island. Pp. 461-466 *in* Symp. on the California islands (D. Powers, Ed.). Santa Barbara, California, Santa Barbara Mus. Nat. Hist.