MALE AND FEMALE PARENTAL ROLES IN THE WESTERN GULL UNDER DIFFERENT ENVIRONMENTAL CONDITIONS

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ABSTRACT.—I examined variation in parental care in the Western Gull (*Larus occidentalis*), spending two seasons on Southeast Farallon Island (SEFI), where the population was large and competition for breeding space appeared to be high. During the first season (1973), food appeared to be less abundant than usual. During 1973, male gulls spent more time on their territories than did their mates. In 1974, food appeared to be more abundant; male and female gulls spent similar amounts of time on their territories, but females spent more time in incubation. Chick survival also increased in 1974. A third season was spent on Santa Barbara Island, where food appeared to be less abundant than on SEFI in either year; population size and density were low, however, and there did not appear to be much competition for breeding space. In this colony, females spent considerably more time both on their territories and in incubation than did their mates.

Male gulls were found to be significantly larger than female gulls in both populations. Male gulls were also more aggressive than females and performed the bulk of territorial defense. Male gulls fed upon larger food items than did females, brought back heavier loads of food, and fed their chicks more often than did their mates. On SEFI, male gulls were monagamous, and nearly all retained the same mate for three consecutive seasons. These males did engage in some promiscuous activity but were rebuffed by females. This activity was more frequent in 1974. On Santa Barbara Island, males participated in considerable promiscuous activity with unmated females and were observed to copulate with females other than their mates. *Received 15 May 1980, accepted 19 February 1981.*

SEVERAL key theoretical papers concerning the evolution of mating systems have stressed the importance of requirements for parental care in determining the degree to which individuals can monopolize either mates or resources (e.g. Orians 1969, Trivers 1972, Emlen and Oring 1977). In particular, Trivers (1972) suggested that the relative parental investments of males and females are crucial in determining whether the species will be polygynous, monagamous, or polyandrous. Emlen and Oring (1977) emphasized that "the degree to which an animal can take advantage of the 'polygamy potential' of the environment depends in large part on the degree of parental care required for successful rearing of the young."

The suggestions are provocative, but actual measurements of relative amounts of parental care by males and females are rare. To test the validity of the suggestions put forth by Trivers and Emlen and Oring, a study should be carried out that asks the question: "Does variation in demand for parental care result in a change in either mating strategy or in the ability of individuals to take advantage of the 'polygamy potential' of the environment?"

Most studies of male-female parental roles are of an "either-or" nature; e.g. the male does or does not incubate. I feel that it is important to quantify parental care by measuring actual amounts of incubation or territorial defense and how these may vary either between years or between populations if we are to understand the subtle causations of changes in the reproductive tactics of a species. [I emphasize "parental care" rather than "parental investment" as suggested by Trivers (1972), because I

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feel that it is possible to quantify such variables as territorial defense, incubation, or chick feeding, but that other variables included by Trivers, such as risk from defending a brood against predation, cannot be measured.]

More than 90% of avian species have been described as monogamous (Lack 1968). This predominance of monogamy among birds is attributed to a "considerable demand for parental care by both parents" (Emlen and Oring 1977), or because "Among birds, the only activity for which males are not equally as adept as females is egg laying" (Orians 1969). As a result, the species of birds that regularly deviate from monogamy have been the basis of considerable study and speculation (Orians 1969, Selander 1972, McLaren 1972, Wittenberger 1976, Altmann et al. 1977, Emlen and Oring 1977). There are also several avian species, however, that have been described as "normally monogamous," in which the males have been observed to show promiscuous behavior on occasion (Gladstone 1979).

These normally monogamous, occasionally promiscuous species are ideal organisms in which to examine variation in parental care. If a reduced demand for male parental care leads to either an increase in promiscuous activity or an initiation of promiscuous behavior by a fully monogamous male, this would provide support for the real applicability of the ideas put forth by Trivers (1972) and Emlen and Oring (1977).

Gulls are ideal organisms on which to conduct observations necessary to test these hypotheses. They are large, monogamous, but known to engage in promiscuous activity (Tinbergen 1960, MacRoberts 1973). They breed in conspicuous, easily located colonies, where all behavior related to the raising of offspring occurs in a relatively small breeding territory. The Western Gull (*Larus occidentalis*) is particularly good for conducting comparative studies between colonies, for it breeds in a variety of habitats under widely varying ecological conditions (Schreiber 1970, Harper 1971, Coulter 1973, Hunt and Hunt 1975).

Study Sites and Methods

The initial 2 yr of this study were carried out on Southeast Farallon Island, which is the site of the largest colony of Western Gulls in existence. A rocky, granitic island, Southeast Farallon and its neighboring islets lie at the western edge of the continental shelf, 43 km due west of San Francisco's Golden Gate (37°24′N, 123°00′W). The Farallones lie within the cold, rich waters of the California Current, which, during the spring breeding season, is one of the most productive zones of upwelling in temperate climes (Bolin and Abbott 1963). Apparently as a result of this, the Farallones are one of the major seabird breeding areas of the north-central Pacific, with 12 species totalling some 250,000 individuals using Southeast Farallon as a breeding site (Ainley and Lewis 1974).

Santa Barbara Island, located in the Channel Islands National Monument, Santa Barbara County, California, is the smallest of the Channel Island group. Santa Barbara Island is located 61 km from the mainland and 39 km from Santa Catalina Island at 33°28′N, 119°02′W. It lies south of Point Conception, where the California Current moves away from the coast into oceanic waters. As a result, upwelling is greatly reduced in this area, and the food supply for seabirds is almost certainly reduced as well. Only six species of seabirds breed on Santa Barbara Island, and of these only the Western Gull (Table 1) and Xantus' Murrelet (*Endomychura hypoleuca*) are common (Hunt and Hunt 1974). The study sites will henceforth be referred to by their initials: SEFI (Southeast Farallon) and SBI (Santa Barbara).

Unusual reproductive anomalies have been observed in the SBI Western Gull population that have not been observed to occur on SEFI. These include supernormal clutches (more than the normal three eggs) (Hunt and Hunt 1973), female-female pairing (Hunt and Hunt 1977), and the existence of a strongly female-biased skewed sex ratio (Hunt et al. 1980). In combination with the large amount of breeding space available and the small gull population, these observations by Hunt and his colleagues suggested that SBI would be an ideal colony for comparison with the colony on SEFI (see Table 1).

My methods of observation were similar at both colonies. Observations were conducted from either

TABLE 1. Comparison of Western Gull colonies on SEFI and SBI.

Site	Total island area (ha)	Size of gull population (pairs)	Territory size		
			n	Mean and SD	Range
SEFI	44	10,000–11,000	33	10.18 ± 3.85 m^2	4.30–20.16 m^2
SBI[a]	260	1,500	39	150 ± 214 m^2	24–803 m^2

[a] Data obtained from Hunt and Hunt (1975).

a blind or natural cover on SEFI from mid-April to late July in 1973 and 1974 and from early June to mid-July on SBI in 1975. Continuous watches were conducted from 0500 until 2000, and the shortest period of continuous observation at either study site was 4 h. During the course of the study, some 1,250 h were spent in observation, yielding data consisting of over 15,000 bird h (observation h times the number of pairs watched per h).

The data collected consisted primarily of time budgets for male and female birds. This included censuses of study plots at 15-min intervals to determine which member or members of a pair were present on the territory and the activities in which they were involved (incubation, foraging, sleeping, etc.). In addition, noteworthy behavior that occurred during the 15-min period, such as feeding of chicks or mate, or aggressive interactions, were recognized. Level 1 encounters, the most intense and time-consuming, were fights and extended aerial pursuits, nearly all of which were directed at intruders. Level 2 indicated lengthy or intense displays, such as grass-pulling (Tinbergen 1960) and short aerial or extended terrestrial pursuits. Level 3 indicated basic displays, e.g. choking, uprights, or vocalizations (see Tinbergen 1959, 1960 for terminology). Also during observation periods, specific food items brought back and fed to chicks were identified using a 15–60 power telescope.

Because 24 pairs were monitored simultaneously on SEFI compared with 6–8 pairs on SBI, some interactions were undoubtedly missed during regular observation periods on SEFI. To correct this problem and to obtain a better index of levels of aggressive interaction in the two colonies, special 2-h observation periods were carried out in both colonies for several days during incubation. During these, the only data collected concerned aggressive interactions. This allowed rapid monitoring in the dense SEFI colony so that fewer interactions were missed.

Individuals on SEFI were sexed by using a combination of methods to eliminate possible ambiguities. During 1973, 36 gulls (15 males, 21 females) were collected for examination of stomach contents and gonadal development. Before collection, all birds were sexed at a distance by using criteria such as the larger size and the larger and heavier bill of males. All birds collected turned out to have been sexed correctly using this method, and there was no overlap between males and females in weight or in the width or depth of the bill at the nares. There was also significant sexual dimorphism in all other dimensions (Table 2).

In capturing birds for sexing by laparotomy, Hunt and his associates obtained similar results on SBI (Table 2; see also Table 1, Hunt et al. 1980). Thus, among all individuals examined in this species, males

TABLE 2. Sexual dimorphism of male and female western gulls.[a]

A. SEFI	Weight (g)	Wing chord (mm)	Culmen (mm)	Bill width at nares (mm)	Bill depth at base (mm)	Bill depth at red spot (mm)
Males (n = 15)	1,136.1 ± 46.9[b]	428.0 ± 10.0[b]	57.2 ± 1.8[c]	13.9 ± 1.6[d]	20.9 ± 0.7[d]	22.3 ± 0.7[c]
Females (n = 21)	878.6 ± 78.2	405.4 ± 7.4	52.9 ± 2.8	9.5 ± 0.5	18.7 ± 0.6	20.4 ± 0.9

B. SBI[e]	Weight (g)	Head length (mm)	Culmen length	Bill depth at red spot
Males (n = 7)	980.7 ± 53.3[b]	126.9 ± 3.2[b]	55.7 ± 1.8[c]	21.7 ± 2.6[c]
Females (n = 31)	768.6 ± 47.1	117.4 ± 2.1	50.2 ± 2.6	19.0 ± 0.6

[a] All units are given as mean ± SD.
[b] Difference between males and females significant at 0.001 level by Wilcoxon signed ranks test.
[c] Difference between males and females significant at 0.05 level by Wilcoxon signed ranks test.
[d] Difference between males and females significant at 0.01 level by Wilcoxon signed ranks test.
[e] All measurements courtesy of Dr. G. L. Hunt, Department of Ecology and Evolutionary Biology, University of California, Irvine.

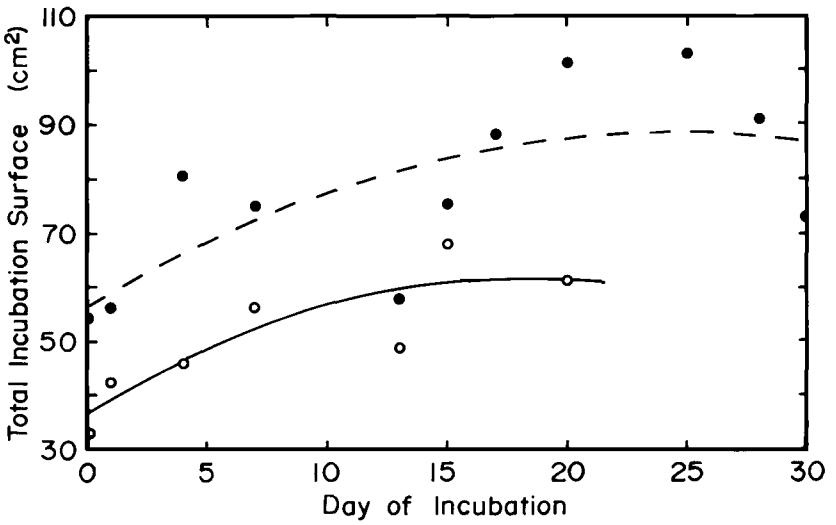

Fig. 1. Comparison of size of brood patches of male and female gulls on SEFI. Area of all three brood patches has been totaled to give total surface area available for incubation. Differences between males and females are significant at the 0.001 level by ANOVA for both total area and individual brood patches (males $n = 7$, females $n = 11$). Curve was fitted to the data using regression.

have proved to be significantly larger than females. In fact, in all investigations of sexual dimorphism in gulls, males have proved to be larger than females, and, in all cases where both members of a pair have been collected, the male has been larger than his mate (Tinbergen 1960, Harris 1964, Harris and Jones 1969, Ingolfsson 1969, Ryder 1978, this study).

In addition, the role taken in courtship-feeding and copulation was noted for individuals in each pair observed during data collection on SEFI. Female gulls have never been reported to mount males, and, because during this study the smaller member of a pair was never observed either feeding or mounting the larger member of the pair, it was assumed that, if one member of a pair was noticeably larger and also courtship-fed and mounted its mate, this bird was a male.

In addition to sex, identifiable characteristics, such as markings on the bill, unusual feather patterns, or holes or tears in the webs of the feet, were noted for each bird. Also recorded for each individual were location of the territory, time of copulation, egg laying, and hatching, and its record of success in fledging chicks. Twelve birds captured using nest traps (Tinbergen 1960) on SEFI were weighed, measured, and color-banded. Males of this group were marked a bright yellow atop the head with picric acid, while females were marked with picric acid on the breast. In all, both individuals were recognizable in 30 pairs on SEFI and in 8 male-female and 3 female-female pairs on SBI. (On SBI, all individuals had been sexed by laparotomy and color banded by Hunt and his associates.)

Results

Sexual dimorphism.—On both SEFI and SBI, males were significantly larger than females in all measurements taken (Table 2). There was no overlap in weight at either colony, and males weighed on the average 25% more than females. Although females were significantly smaller than males in all other characters, however, their brood patches were significantly larger than those of males at all stages of the breeding season (Fig. 1).

Reproductive behavior during the pre-egg-laying period (SEFI).—Female Western Gulls on SEFI spent most of their time on their territories during the 2 weeks prior to the onset of egg laying. In contrast, male gulls spent considerable amounts of time away from the territory (Table 3). These males were presumably out at sea

TABLE 3. Male and female activities during the prelaying period.

	Percentage of TOT present on territory[a]	Number of aggressive interactions/h		
		Level 1	Level 2	Level 3
SEFI (1974)				
Males (n = 22)	54.8[b]	0.14[c]	0.48[c]	0.35[c]
Females (n = 22)	93.6	0.02	0.06	0.12
SBI (1975)[d]				
Males (n = 8)	46.3[b]	0.09[c]	0.37[c]	0.33[c]
Females (n = 8)	75.6	0.00	0.03	0.23

[a] TOT = total observation time in bird hours (actual number of hours observed = TOT/n pairs observed). [TOT: SEFI (1974) = 546 h; SBI (1975) = 41 h]
[b] male ≠ female ($P < 0.01$ by t-test): statistics were carried out on actual measurements of time.
[c] Male ≠ female ($P < 0.01$ by Wilcoxon signed ranks test).
[d] All data courtesy Paul Ewald, Museum of Zoology, University of Michigan, Ann Arbor.

foraging, because they fed their mates at least two or three times a day during this entire period.

Competition for nesting territories appeared to be quite vigorous on SEFI. As a result, it was probably advantageous for one member of the pair to remain on the site at all times. Out of 19 vigorous fights witnessed during April 1974, 16 involved intruding birds that had established themselves on a territory during the absence of the resident pair. In contrast, there were no fights and very few level 1 interactions at the time the intrusion occurred. Aggressive interaction, especially of levels 1 and 2, primarily involved males during the prelaying period, despite the observation that females spent nearly twice as much time on the territory during this period (Table 3). About 70% of female aggressive acts occurred while the male was absent from the territory. Those acts of aggression performed by females while their mates were present were almost always performed in tandem with the male.

Both sexes appeared to participate equally in the selection of the nest site and the construction of the nest cup. Pairs of Western Gulls on SEFI are very site-tenacious. Of thirty pairs monitored over the course of 3 yr (1973–1975), 26 pairs remained mated and on the same territory. Twenty-five of these pairs even used the same nest site for the 3 yr.

Reproductive behavior during the prelaying period (SBI).—Unfortunately, I was unable to spend any time on SBI during the prelaying period of 1975. Some data concerning male-female behavior were made available by P. Ewald (pers. comm.). As on SEFI, female gulls on SBI spent more time on the territory than their mates did, but the difference was less marked on SBI (Table 3). Females were fed by males, but the data are too few to determine whether this is an important source of nourishment or the females also spend considerable amounts of time foraging for themselves, especially because females on SBI were present a lower percentage of the total observation time (TOT) than were females on SEFI.

Aggressive activity was less frequent than on SEFI (Tables 3 and 4), but males were again the primary aggressors. Out of 53 encounters witnessed by Ewald, 45 involved the male of the pair (Table 3).

Behavior during incubation (SEFI).—Through careful observations of individuals on SEFI, some probable environmental influences on patterns of incubation attentiveness in male and female gulls were discovered. In 1973, males and females spent almost exactly the same amounts of time in incubation, although males actually spent more time in total on the territory during this period (Table 5).

TABLE 4. Comparative levels of aggressive interaction between SEFI and SBI.[a]

	Number of interactions[b]	Number/pair/h[c]
SEFI (n = 24 pairs)	285[d]	1.98
SBI (n = 13 pairs)	25	0.32

[a] All data collected during incubation period over three separate 2-h periods on each colony.
[b] Number of interactions = total number of aggressive acts by all pairs.
[c] Number/pair/h = mean number of interactions that a given pair (male and female) were involved in per hour.
[d] Differences between SEFI and SBI significant at 0.001 level by χ^2 test.

During the 1974 incubation period, male and female gulls on SEFI spent approximately equal amounts of time on the territory; females, however, spent significantly more time in incubation than did males (Table 5). There was also a change in the frequency of aggressive behavior. In 1973, when males spent more time in incubation due to the absence of their mates, the ratio of male to female aggressive acts was lower than in 1974 (about 3:1 in 1973, compared with 5:1 in 1974; Table 5). Both male and female gulls spent more total time on their territories in 1974 than in 1973 (Table 5).

Therefore, it appears that female gulls on SEFI will carry out the majority of incubation when conditions allow. In fact, female gulls may actually spend more time in incubation than the data show. On a few clear, moonlit nights, with the help of an ambient-light magnifying "starlight scope," it was possible to carry out about 15 h of observation, during which 95% of the birds identified on nests were females.

Western Gulls on SEFI were strongly monogamous. Some males did show a tendency toward promiscuity, however, by attempting to force copulation with (or "rape") females on neighboring territories. Such behavior occurred almost exclusively during the latter parts of the prelaying period and the early stages of incubation. Female gulls invariably offered violent resistance to these attempts. Out of 114 attempted forced copulations witnessed on SEFI, only one successful cloacal contact was seen. Rapists were always males whose mates were either just about to lay or who had just laid their eggs. These attempted "rapes" were much more common in 1974 than in 1973. Out of the observed 114 attempts, 26 occurred in

TABLE 5. Male-female activity budgets during incubation.

	Percentage of TOT present on territory[a]	Percentage of TOT spent in incubation[a]	Number of aggressive interactions/h		
			Level 1	Level 2	Level 3
SEFI (1973)					
Males (n = 24)	67.9[b]	50.4	0.15[c,d]	—	—
Females (n = 24)	58.9	49.6	0.05	—	—
SEFI (1974)					
Males (n = 24)	77.0	41.6[b]	0.09[d]	0.20[d]	0.11[d]
Females (n = 24)	77.7	58.4	0.02	0.02	0.03
SBI (1975)					
Males (n = 6)	56.4[b]	28.5[b]	0.01	0.15[d]	0.12[d]
Females (n = 6)[e]	91.2	71.5	0.00	0.01	0.03

[a] TOT = total observation time as in Table 3: SEFI (1973) = 2,516.5 h; SEFI (1974) = 1,218.0 h; SBI (1975) = 448.0 h.
[b] Males ≠ females ($P < 0.001$ by t-test).
[c] Levels of intensity were not distinguished in 1973; all are included as level 1.
[d] Males ≠ females ($P < 0.001$ by Wilcoxon signed ranks test).
[e] No females from female-female pairs are included.

TABLE 6. Male and female activities during chick period.

	Percentage of TOT present on territory[a]	Chick feedings per adult/observation day[b]	Number of aggressive interactions/h		
			Level 1	Level 2	Level 3
SEFI (1973)					
Males (n = 26)	59.7[c]	2.21[d]	0.35[e,f]	—	—
Females (n = 26)	48.0	1.84	0.27		
SEFI (1974)					
Males (n = 28)	65.6	3.38[d]	0.13[d]	0.17[d]	0.41[d]
Females (n = 28)	63.9	2.60	0.06	0.09	0.31
SBI (1975)					
Males (n = 6)	58.0[c]	2.17[d]	0.06[d]	0.10	0.14[d]
Females (n = 6)	68.1	1.22	0.01	0.10	0.05

[a] TOT = total observation time (as in Tables 3 and 5). TOT: SEFI (1973) = 3,500.5 h; SEFI (1974) = 6,340.0 h; SBI (1975) = 414.0 h.

[b] Chick feedings represent each time a parent returns from a foraging bout and feeds its chicks; does not include repeat feedings from same load (observation day = 15 h).

[c] Males ≠ females ($P < 0.01$ by t-test).

[d] Males ≠ females ($P < 0.05$ by Wilcoxon signed ranks test).

[e] Levels of intensity were not distinguished during 1973; all are included as level 1.

1973, compared with 88 in 1974 during less than half as many hours of observation (Table 5).

Behavior during incubation (SBI).—Female gulls on SBI perform an even higher percentage of the incubation duties than do females on SEFI. The average female gull on SBI spent 1.6 times as much time on the territory as her mate did and over 2.5 times as much time as her mate in incubation (Table 5). Female gulls on SBI also spent a considerably greater percentage of the total observation time incubating than did females on SEFI, whereas their mates spent considerably less time.

Despite the fact that they were present significantly less often on the territory than were females, male gulls on SBI were still involved in many more aggressive interactions during the incubation period. Male Western Gulls on SBI were involved in 72 of 96 aggressive encounters observed during this period (Table 5). On SBI, the large size of the territories (Table 1) and the absence of competition for nest sites apparently reduced the need for territorial defense. Aggressive interactions were less frequent on SBI than on SEFI as a result (Table 4). Intruder pressure was also much lower on SBI than on SEFI, as demonstrated by the lower frequencies of level 1 interactions (Tables 3, 5, and 6). In addition, the likelihood of "rape" was much lower than on SEFI, due to the increased distance between neighbors and, perhaps more important, to the female-biased, skewed sex ratio present on SBI (Hunt et al. 1980).

While female gulls on SBI diligently attended their nests, some males spent considerable amounts of time either on the "club" areas (see Tinbergen 1960 for definition) or engaged in other activities away from the breeding territory. On the "clubs," however, these males did not generally preen or rest as described by Tinbergen (1960). Instead, they frequently interacted aggressively, appeared to defend a personal space, and frequently attempted to court and copulate with any female (presumably unmated) that appeared willing. Males not on the clubs frequently solicited copulations as well, generally from members of the female-female pairs, which had breeding sites located among the breeding territories of the male-female pairs. On eight separate occasions, male gulls known to be mated to females with

whom they already had either eggs or chicks were observed to court, copulate with, and desert females while their mates were visible either on a nest or the breeding territory during the entire proceedings. Other, unidentified, male gulls were observed to copulate with female gulls either on the club area (12 times) or on the territories of female-female pairs (four times). The last such occurrence was witnessed in late June, when over 90% of the breeding pairs on SBI had already hatched chicks. (See Hunt and Hunt 1975 for timing of reproduction in this population.) No behavior of this kind was ever observed to occur on SEFI.

After a successful copulation with a female other than his mate, seven of the eight known males returned immediately to the breeding territory. On those occasions when the deserted female attempted to follow the male back to his territory, the males displayed very ambivalent behavior, such as head-tossing (a precopulatory display) mingled with aggressive uprights (threat display) and outright attacks, while their mates remained on the nest. One female gull on SBI apparently died as a result of such an attack. When autopsied, she showed no evidence of either brood patches or regressed follicles, so she had apparently not bred during the 1975 season.

Behavior during the chick period (SEFI).—The hatching of the first chick was considered to be the beginning of the chick period, because feeding of chicks begins and incubation behavior declines rapidly after this point. Both male and female Western Gulls became more aggressive once chicks had hatched than they had been during the incubation period. Females, in fact, became more aggressive than they had been in any previous period, whereas males were slightly less aggressive than during the prelaying period, when male aggression appeared to peak (Table 6; cf. Tables 3 and 5).

Despite the increase in female aggressive activity, the average female gull on SEFI only participated in about half as many aggressive acts as an average male during this time (Table 6), and males still carried out most aggressive acts when both members of the pair were present. In fact, during this period and during incubation, female aggressive activity did not appear to be related to the territory, but rather to the nest and the chicks and their immediate vicinity, whereas males continued to defend their territorial boundaries.

Attentiveness to the territory changed with the hatching of the eggs. During incubation (especially in 1974), both the male and female of a pair were often on the territory together, usually with the female on the nest, while the male either patrolled the area or rested nearby. As soon as the chicks hatched, however, generally only one adult would be present, with the other presumably foraging to feed the chicks.

Male Western Gulls on SEFI generally fed their chicks larger food items than did their mates (Fig. 2). Male gulls also brought back heavier loads of food than did their mates. Male loads ($n = 8$; $\bar{x} = 130$ g, range = 87–179 g) were much larger on average than those of their mates ($n = 6$; $\bar{x} = 97$ g, range = 67–129 g). This is not surprising in view of the fact that male gulls were significantly larger than females. Besides taking smaller food items, female Western Gulls on SEFI also appeared to require more time to forage than males. During 1973, female gulls spent an average of 3.7 ± 0.9 h per foraging trip ($n = 112$), compared with only 2.1 ± 0.4 h per trip for males ($n = 130$; $P < 0.001$ by Mann-Whitney U-test). (A foraging bout was measured as the period from departure from the nest until return with food. If no food was brought, an absence was not considered a foraging bout.) In 1974, females spent an average of 2.6 ± 0.7 h per foraging trip ($n = 226$), while male foraging times also declined to an average 1.8 ± 0.6 h ($n = 342$; $P < 0.01$ by Mann-Whitney).

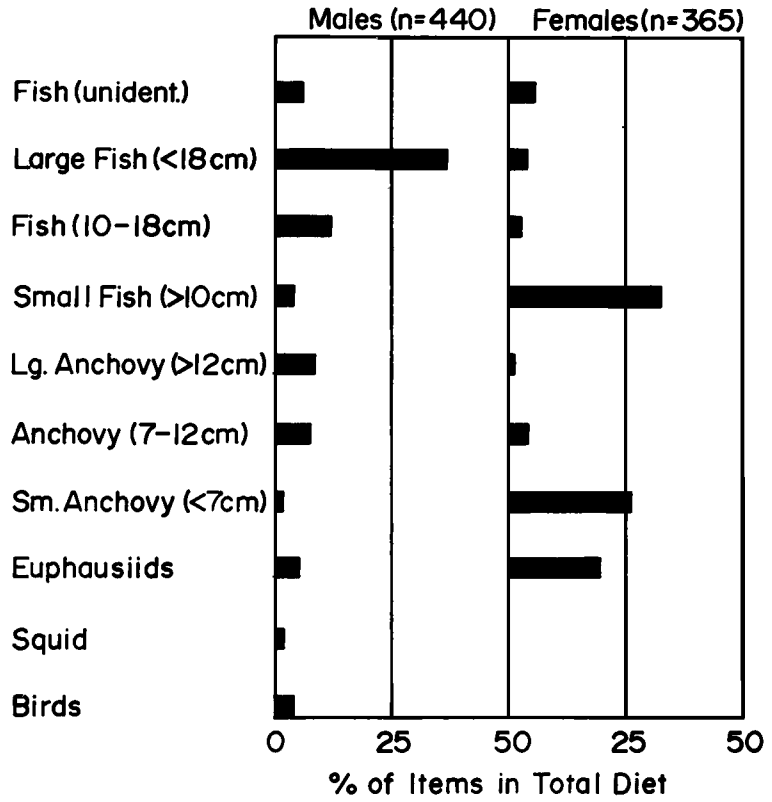

Fig. 2. Food items observed being fed to chicks by male and female gulls on SEFI during chick period of 1974 breeding season (n = individual feedings).

In both years of the study, male gulls fed their chicks significantly more often on average than did their mates (Table 6). The same basic pattern existed in territorial attendance, however, that had been observed during incubation: during 1973 males spent significantly more time on territory than did their mates, whereas in 1974 there were no significant differences in male and female attendance (but see Piracy, below, for a possible explanation).

Behavior during the chick period (SBI).—Once chicks were present, male Western Gulls on SBI became much more attentive than they had been during previous periods. Females were still present on the territory significantly more often than males during the chick period (Table 6), but the difference was far less than was the case during incubation. On SBI, male gulls may be absent more than females while chicks are present, partly because it takes more time for them to forage, which is the reverse of the situation on SEFI. Female foraging bouts ($n = 22, \bar{x} = 2.1 \pm 0.7$ h) were significantly shorter ($P < 0.05$ by Wilcoxon rank sum) than male foraging bouts ($n = 31, \bar{x} = 3.25 \pm 0.3$ h). Despite the fact that it apparently required more time for males to forage on SBI, male gulls in this population still fed their chicks significantly more often than did their mates. As on SEFI, male gulls on SBI fed their chicks larger food items than did female gulls (Fig. 3). I was not able to obtain food-load sizes on SBI. However, because in this population males were also signifi-

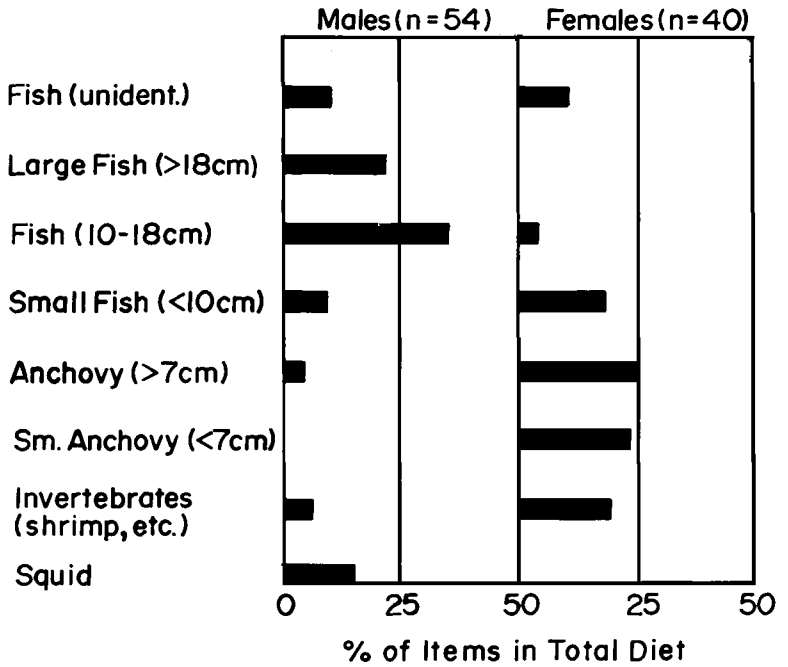

Fig. 3. Food items observed being fed to chicks on SBI by male and female gulls during chick period of 1975 breeding season.

cantly larger than their mates and brought in larger food items as well, it seems likely that male food loads were larger than those brought in by females.

During the chick period on SBI, the size and shape of the breeding territory may change considerably (see Hunt and Hunt 1975 for detailed descriptions), apparently because the area defended by the parents becomes centered around the chicks, as on SEFI. Some pairs whose territories adjoined club areas wandered unresisted through the clubs, accompanied by their chicks. As on SEFI, the level and frequency of aggression increased during the chick period, especially in males (cf. Tables 5 and 6), and males were significantly more aggressive than females. Frequency of aggression was, however, much lower than on SEFI during the chick period. During the 1975 breeding season on SBI, only three attacks on chicks, either by neighbors or intruders, were observed. On SBI, chicks of less than 2 weeks of age could remain unattended on the club area in the presence of many adults other than their parents without being attacked.

Piracy on SEFI.—In 1973 during the chick period, male gulls were present significantly more often on the territory than were their mates (Table 6). As this period progressed, from one to as many as five other adult gulls would swoop in and attempt to steal the food 80% of the times (765 out of 944) that an adult gull returned to the territory and attempted to feed its chicks. Generally, a wild melee ensued, with adults and chicks all contesting for a large fish or other food item. As a result of these depredations, the colony was in an almost constant state of agitation, and many birds began to appear somewhat the worse for wear. All of the pirates were male birds and were usually nearby neighbors of the victims. Some males were observed to pirate continuously, others only sporadically, and some never pirated

TABLE 7. Behavioral comparison of pirate and nonpirate pairs during the chick period of 1973 on SEFI.[a]

	Pirate males (n = 11)	Nonpirate males (n = 15)	Pirate females[b] (n = 11)	Nonpirate females (n = 15)
Amount of time present on territory (min)	5,558 ± 609.5	4,699[c] ± 720.1	3,785 ± 580.9	3,691 ± 512.3
Mean number of aggressive interactions observed	31.7 ± 10.1	25.4 ± 8.1	16.3 ± 11.0	18.2 ± 9.7
Mean number of chick feedings	18.9 ± 9.1	20.5 ± 6.8	14.5 ± 5.1	19.3[d] ± 3.9
Mean breeding success (number of chicks fledged nest)	—	—	1.09 ± 1.13	1.85[e] ± 1.61

[a] All values in Table are mean values per bird or per pair.
[b] Pirate females are mates of pirates and did not pirate themselves.
[c] Difference between pirates and nonpirates significant at the 0.02 level by t-test.
[d] Difference between pirates and nonpirates significant at the 0.05 level by t-test.
[e] Difference between pirates and nonpirates significant at the 0.0005 level by Fisher's exact test.

at all. Pirate males differed behaviorally from nonpirates in a number of ways (Table 7). Pirate males spent significantly more time on their territories than did nonpirate males. Females mated to nonpirate males spent nearly as much time on the territory as did their mates, whereas the mates of pirate males spent significantly less time on their territories than did the pirates. This indicates that overall differences in male and female attentiveness to the territory during the chick period of 1973 were due primarily to pirate males.

Pirates and nonpirates also differed, although not as significantly, in frequency of aggressive acts and chick-feedings (Table 7). Pirate males were the most aggressive birds during the chick period of 1973, and their mates were the least aggressive. Both males and females of nonpirate pairs fed their chicks more often than did pirate males, who, in turn, fed their chicks more often than did their mates. Pirate pairs were relatively unsuccessful as parents, fledging (chick able to fly independently) only 50% of their hatchlings, compared with 70.5% for nonpirates. Pirates generally lost their offspring early in the chick period and then turned to piracy (see also Pierotti 1980).

In 1974, piracy was greatly reduced (27% of feedings; 682 out of 2,528). No males were full-time pirates, and only nine males practiced any piracy at all. These males were again less successful as parents, fledging only 1.4 chicks per nest, compared with 2.1 chicks per nest among nonpirates. Overall in 1974 most pairs behaved as the nonpirate pairs had in 1973 (cf. Tables 6 and 7). Some males that had been successful in 1973 (at least two chicks fledged) had fewer offspring in 1974 and began pirating part-time. Others who had been pirates in 1973 had significant increases in the number of surviving offspring and ceased pirating (Pierotti 1980).

Comparative breeding performance.—During 1973, the number of chicks fledged per nest on SEFI was the lowest of the 4 yr for which data were available (Table 8). Clutch size and the number of eggs hatched per nest were comparable to the other years. In 1974, the number of chicks fledged per nest increased significantly ($P < 0.001$, t-test).

On SBI, the number of chicks fledged per nest was generally higher than on SEFI. Despite a lower mean clutch size than that observed in any year on SEFI, the eight male-female pairs of Western Gulls on SBI had 100% hatching success and fledged more chicks per pair than pairs on SEFI did in any year but 1974 (Table 8).

TABLE 8. Comparative breeding performances of Western Gulls on SEFI and SBI.

	$\bar{x}$ clutch size	$\bar{x}$ eggs hatched per nest	$\bar{x}$ chicks fledged per nest	Chicks fledged/ eggs hatched (%)	Chicks fledged/ eggs laid (%)
SEFI					
1971 (n = 91)[a]	2.81	2.20	1.91	86.8	68.0
1972 (n = 94)[a]	2.72	2.25	1.91	84.8	70.2
1973 (n = 26)	2.81 ± 0.63	2.37 ± 0.82	1.54 ± 0.94	65.0	54.8
1974					
Study area (n = 24)	2.83 ± 0.67	2.25 ± 0.61	2.04 ± 0.77	90.7	72.1
Other areas (n = 151)	2.89 ± 0.41	2.47 ± 0.77	2.25 ± 0.91	91.1	77.5
SBI					
1972 (n = 39)[b]	—	2.53	2.15	84.8	—
1975 (n = 8)	2.67 ± 0.81	2.67 ± 0.81	2.25 ± 0.95	84.3	84.3

[a] Data from Coulter (1973).
[b] Data from Hunt and Hunt (1975).

DISCUSSION

The year 1973 was unusual throughout the entire California Current system. Water temperatures were unusually high, and overall productivity was low during the spring and summer (Ainley and Lewis 1974). In 1974, however, water temperatures were consistently lower than average during March through July, and food was apparently abundant around SEFI (D. G. Ainley pers. comm.). This apparent variation in food availability was reflected in the breeding biology and parental roles of Western Gulls on SEFI. In 1973, the reduced availability of food apparently caused females to be absent from their territories a greater percentage of the time than in 1974. They apparently spent this time foraging, because the average female foraging bout was more than an hour shorter in 1974 than in 1973. The absence of the females meant that males had to spend a greater percentage of their time incubating in 1973 than in 1974 (Table 5).

In 1974, with food apparently much more available, both sexes spent more total time present on their territories during both the incubation and chick periods. During the 1974 breeding season, females also spent much more time incubating than they had in 1973. Male gulls, freed from incubation duties, showed higher frequencies of aggressive interactions (Table 5) and engaged in more promiscuous activity, as evidenced by the fact that more than three times as many attempted "rapes" were observed in 1974 than in 1973. This suggests that a reduced demand for male parental care, i.e. incubation, may lead to an increase in promiscuous activity on the part of male gulls. In addition, evidence that the food supply for Western Gulls in 1973 on SEFI was lower than in 1974 comes from the observation that both male and female foraging bouts were shorter in 1974. Also, piracy was much more frequent in 1973 than in 1974, and the number of chicks fledged per pair was significantly higher in 1974 than in 1973 (Table 8).

Although the number of chicks fledged per nest on SBI is as high or higher than on SEFI (Table 8), the food supply is probably poorer around SBI. This is indicated by the small size of the breeding seabird populations on SBI and the observation that water temperatures tend to be higher and upwelling greatly reduced in the Bight of Southern California (Bolin and Abbott 1963). Male gulls, in particular,

apparently must travel long distances to obtain food. This is indicated by their long foraging bouts and observations from radio-tracking (K. T. Briggs pers. comm.) that male Western Gulls fly much farther from nearby San Miguel Island on foraging trips, sometimes traveling as far as 40 km from the island, whereas female gulls rarely travel more than 2–3 km offshore. Regardless of the cause, however, the small population size on SBI has resulted in reduced intruder pressure and competition for space compared to SEFI. This is shown by the lower frequency of aggressive interactions (especially level 1) on SBI (Tables 3–6).

Despite the apparent effects on reproductive behavior of male and female gulls caused by variations in food supply between 1973 and 1974 on SEFI, and on SBI in 1975, specific and well-defined roles in parental care can be described for each sex. During the prelaying period, males expend considerable amounts of energy in the establishment and defense of a territory. According to the strict definition of parental investment by Trivers (1972) as "any investment by the parent in an individual offspring that increases the offspring's chances of survival at the cost of the parent's ability to invest in other offspring," territorial defense does not qualify as parental investment. As the size of the territory may have a marked effect on subsequent chick survival (Hunt and Hunt 1976), however, I chose to include aggressive behavior by male (and female) gulls as parental investment.

The additional energy expended by a male in acquiring food for the female during egg formation is also a probable contribution toward the future survival of his offspring. Courtship feeding is widespread among birds and may continue throughout incubation (Lack 1968). Several investigators have noted extensive courtship feeding in several species of larids and have suggested that this may be an important source of energy to the female during egg formation (Cullen and Ashmole 1963, Brown 1967, Nisbet 1973). Brown (1967) has estimated that in the Lesser Black-Backed Gull (*Larus fuscus*) the female must produce about 42% of her body weight in egg formation and related processes over a period of about 10 days. King (1973) calculated that egg formation in species with precocial offspring, such as gulls, may require an increase in daily energy intake of more than 30% above normal. Therefore, if the male can obtain enough food for both himself and his mate, it is almost certainly to their advantage to have her remain on the territory and act as a sentry while conserving energy for reproduction.

The female has relatively little to do with the defense and establishment of the territory during the prelaying period, but she must commit a large amount of energy to egg production. Because this commitment is probably greater than any single expenditure the male can make, this period is crucial in determining the breeding system of the species involved. If little or no further male parental care is required, polygyny will be favored, with the male devoting his subsequent attentions to other females (Orians 1969, Trivers 1972, Emlen and Oring 1977). If, however, considerable male parental care is still required after egg laying, monogamy is likely to be favored, with the rigor of the pair bond increasing with increased demand for male investment.

During incubation, the female is more attentive to the eggs, while the male is still largely involved in the defense of the territory and his mate, provided circumstances do not require his performing a larger share of incubation. Female gulls are adapted to perform the bulk of incubation. Although female gulls are smaller than males, they have significantly larger brood patches (Fig. 1). The male is by far the more aggressive of the pair, and at no time is this trend more marked than during incu-

bation. On SEFI, females threatened only timid-appearing intruders or neighboring females and almost never challenged neighboring males. When the female was present and the male was incubating, if an aggressive intruder landed on the territory, the female would relieve her mate at the nest and free him to deal with the intruder rather than attempting any aggression herself. On SBI, where intruder pressure was very light compared with SEFI (level 1 encounters were much more common on SEFI), males were largely freed from the responsibility of defending the territory. Females in both populations would not fight except in self-defense or when their chicks were attacked; however, they may actually be more aggressive than males when the young are endangered.

The male plays a dominant role in the feeding of the offspring. Not only did males feed the chicks more often than did the females (Table 6), but they brought in larger food items and heavier loads as well (Fig. 2 and 3). This, together with the fact that the male provisions the female extensively in the prelaying stage, indicates that male gulls are responsible for the bulk of their offspring's nutritional requirements.

The absence of male Western Gulls from their territories on SBI apparently cost them little or nothing in terms of fitness, for they were as successful at fledging offspring as male gulls on SEFI during 1974, the year of highest breeding success on SEFI (Table 8). As a result, any offspring that resulted from extra-pair copulations would add to the fitness of these males with only minimal costs.

Two attributes of the SBI Western Gull population are unknown in any other seabird population that has been previously described. These are: (1) the skewed sex ratio, which may be biased in favor of females by more than 1.5:1 (Hunt et al. 1980); and (2) the promiscuous or quasi-polygynous breeding system in which males pair with one female, while copulating with other females, which they subsequently desert. These deserted females may join together in an effort to raise the offspring which result from these liaisons. The major question concerning the SBI Western Gull population is then: "How did the skewed sex ratio arise?" Once a skewed sex ratio exists, female-female pairing is an obvious strategy to appear, because it presents an opportunity to reproduce to individuals that might not otherwise be able to do so.

Even in a strongly monogamous population of gulls such as on SEFI, there can be considerable sexual selection (Darwin 1871, O'Donald 1972). As previously noted, male gulls are larger than females in both populations, yet the breeding strategies of the males appear to be rather different. This is because on SEFI male Western Gulls have a well-defined parental role in which they must forage for the female and the young and defend the territory. Smaller or less aggressive males may be less able to function in this role (O'Donald 1972).

The two basic selection pressures, female choice and male-male competition, that act to promote sexual dimorphism (Darwin 1871, Trivers 1972) appear to work in concert in the Western Gull. Female gulls may select mates that have potential to be good parents (Trivers 1972: 171–172), yet a major criterion for good parenthood, at least on SEFI, is the ability to win at male-male competition for space. On SBI, even though every adult male can hold a territory and find a mate, stronger individuals may be able to control larger areas or areas in proximity to the clubs, where they might have more opportunities to mate with unpaired females.

Male Western Gulls on SBI may take in a higher concentration of pesticides by feeding at a higher trophic level than the females. Male Western Gulls feed at the same trophic level as California sea lions, Brown Pelicans (*Pelecanus occidentalis*),

and Double-Crested Cormorants (*Phalacrocorax auritus*), all of which have experienced pesticide-induced reproductive failures in the last decade in southern California waters (Risebrough et al. 1971, Risebrough 1972, DeLong et al. 1973, Gress et al. 1973). Female gulls, in contrast, feed at a lower trophic level, more comparable to the local Alcidae [Pigeon Guillemot (*Cepphus columba*) and Xantus' Murrelet], which are not known to have experienced reproductive difficulties due to pesticides.

The possibility of pesticide contamination is of particular significance in light of the results of Fry and Toone (1979). These investigators have demonstrated that fresh-egg concentrations of 20–100 ppm o,p'DDT cause feminization of the testes of male California Gull (*Larus californicus*) embryos. This presumably occurs because o,p'DDT acts as an estrogen mimic. If similar phenomena have occurred in the Western Gull, this could explain the skewed sex ratio observed on SBI, because feminized males would not participate in breeding. Similar studies are currently being conducted on Western Gull eggs (D. M. Fry pers. comm.).

Another possibility, albeit a remote one, is that some male gulls may not choose to live in southern California waters with their reduced food supply. In pinnipeds, there is a marked migration of males northward along the Pacific coast at the end of the breeding season (Bartholomew 1970), so that male ranges are, on average, well to the north of those of females of the same species. Western Gull males may move to the north outside of the breeding season, where the larger food items they prefer are more plentiful, and some simply may not return in the spring.

Whatever the causes, Western Gulls on SBI have an unusual breeding system, in which one male may form both a monogamous pair-bond and temporary promiscuous associations with other females. Trivers (1972) predicted that, "In species with strong selection for male parental care, it is more likely that a mixed strategy will be the optimal male course: to help a single female raise young, while not passing up the opportunity to mate with other females whom he will not aid." It is to the advantage of a male to copulate with other females in an effort to maximize his contribution to the gene pool. This may also be the motivation behind the attempted "rapes" observed on SEFI, only in that population the females were unwilling. On SEFI, however, even in 1974 male gulls could not leave their territories unattended to seek unmated females on club areas because of the threat of "rape" by neighbors and the greater intruder pressure, which posed a threat to their territories, mates, and offspring. The situation on SBI may be unfavorable to unpaired (to males) females, but it is apparently preferable to being unable to participate in reproductive activities at all. Even if unsuccessful, a female may still gain experience that could help her to raise future young, as Coulson (1958, 1960) has found in the kittiwake.

Gladstone (1979) has argued that, in most instances of promiscuous behavior by males of normally monogamous species of bird, females defend themselves against forced extra-pair copulations ("rapes") in order to maintain their pair-bond and to protect the investment of their mates. Gladstone further contends that female energetic investment in offspring does not necessarily outweigh that of the male in most of these species. I agree with both of these arguments of Gladstone's, and I feel that they are certainly applicable to the Western Gull population on SEFI. I believe, however, that if male and female energetic investments in offspring are similar on SEFI, male Western Gulls on SBI clearly invest less than their mates. As a result, these males have surplus time and energy to invest in promiscuous activity. The skewed sex ratio on SBI is probably necessary, however, for this promiscuous activity to be successful.

A shortage of males may be more widespread among gulls and other seabirds than is generally supposed (see also Coulson and Wooller 1976). On SEFI in 1975, several adult females on club areas were observed participating in paired behavior and copulating with immature males in third-year plumage (see Dwight 1925). Perhaps more significantly, male gulls that lost their mates always remated within a day or two, sometimes even inducing their new mates to help them raise the offspring of the previous mate, whereas female gulls that lost their mates were unable to remate (Pierotti 1980). Also, reports of polygynous behavior and female-female pairings have appeared in the years since this study was conducted (Shugart and Southern 1977, Ryder and Somppi 1979, Conover et al. 1979). Facultative polygyny and promiscuity may occur fairly regularly in seabirds and should be looked for in future investigations.

The results obtained in this study generally provide support for the ideas put forth by Trivers (1972) and Emlen and Oring (1977); that is, reduced demand for male parental care can lead to a change in the reproductive tactics of male gulls. These males then have a greater opportunity to exploit the "polygamy potential" of their environment. The greater promiscuous activity by male gulls on SEFI in 1974 was largely unsuccessful. The skewed sex ratio on SBI allowed males to obtain "extra-pair" copulations, however, and to become functionally polygynous.

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The Canadian Wildlife Service has translated two Scandinavian books on seabirds: the seabird chapters of Finn Salomonsen's "Fuglene på Grønland" ("The birds of Greenland"; 1967, Rhodos, Copenhagen) and "Barentshavets sjøfuglressurser" by M. Norderhaug, E. Brun, and G. U. Møllen ("Seabird resources of the Barents Sea"; 1977, Norsk Polarinstitutt, Oslo). Copies may be obtained from **Dr. R. G. B. Brown, Canadian Wildlife Service, Bedford Institute of Oceanography, P.O. Box 1006, Dartmouth, Nova Scotia B2Y 4A2, Canada.** The edition is limited and requests from libraries and institutions will be given priority.

The main themes of the Second Nordic Congress of Ornithology, held in Norway in August 1979, were seabirds, tits, duck breeding biology, wader breeding biology, and migration and bird conservation. Twenty of the 59 papers presented at the congress, plus summaries of those published elsewhere, have been published as proceedings of the congress. Copies may be purchased from the **Norwegian Ornithological Society, Innherredsveien 67A, N-7000 Trondheim, Norway.** An international cheque for $28 a copy should be included with each order.