

the 20 days of observation. These birds hovered below the undersides of leaves and snatched the insects.

Trogon were never seen perched near the ground (perching range 3–15 m) and never perched close to another trogon (minimum distance between individuals, 50 cm). Intraspecific aggressions were seen only twice and involved male-female interactions [trogon apparently breed later in the year (June–July; data from specimens of the bird collection at the Instituto de Biología)]. No interspecific aggressions involving a Citreoline Trogon were recorded.

The fruits used by the Citreoline Trogon in the study area were used by other bird species (Table 3). The Grayish Saltator (*Saltator coerulescens*) commonly used all species of fruits. The Yellow-winged Cacique (*Cacicus melanicterus*) was common at *F. pertusa* and *T. octandrum* and occasional at *R. mexicana*, but was absent at *C. engleriana*. In *R. mexicana* the caciques were wasteful feeders, stripping the fleshy part of the fruits without swallowing the seed and dropping many half-eaten fruits to the ground below the parent tree. Wagler's Chachalaca (*Ortalis poliocephala*) consumes figs and fruits of *C. engleriana* and *R. mexicana* (S. Bullock pers. comm.), but we did not observe the species feeding from *F. pertusa* or from *C. engleriana*; chachalaca activity in *R. mexicana* was confined to the early morning and dusk.

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### Morphology and Physiology of Female-female Pair Members

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Female-female pairing has been documented in Western Gulls (*Larus occidentalis*), California Gulls (*L. californicus*), Ring-billed Gulls (*L. delawarensis*; Hunt and Hunt 1977, Conover et al. 1979, Ryder and Somppi 1979), Herring Gulls (*L. argentatus*; Fitch 1979), and Caspian Terns (*Sterna caspia*; Conover 1983). It generally is believed that this type of pairing is a response to a shortage of adult males in the breeding population (see Hunt and Hunt 1977; Ryder 1978a; Conover et al. 1979; Hunt 1980; Hunt et al. 1980; Wingfield et al. 1980a; Kovacs and Ryder 1981, 1983; Fox and Boersma 1983; Lagrenade and Mousseau 1983; Conover 1984a, b). Conover and Hunt (1984) showed that the incidence of female-female pairing increased in California and Ring-billed gull colonies after the removal of breeding-age males.

The occurrence of such an imbalance in undisturbed colonies is thought to be related to differential male mortality. Male gulls may be subject to higher mortality rates than females because of stress related to the acquisition and defense of territories (Coulson and Wooller 1976, Hunt 1980, Hunt et al. 1980). It also has been suggested that toxic chemical contaminants may contribute to reduced male survivorship relative to females through physiological differences between the sexes in lipid and lipophilic toxic chemical dynamics (Wurster et al. 1965, Gish and Chura 1970, Shugart 1980, Conover 1984b). Fry and Toone (1981) injected DDT at concentrations comparable to those found in wild seabird eggs and reported a developmental feminization of testicular tissues of gull embryos to the extent that these individuals would be unable to breed as adults.

Mating systems often are discussed in terms of sexual selection, acting such that females choose among a group of available, often competing, males (Darwin

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TABLE 1. Size, weight, and condition index of female Ring-billed Gulls from male-female and female-female pairs.

	Male-female pairs	Female-female pairs	
Weight (g)	469.0 ± 34.1 (28) <sup>a</sup>	470.3 ± 33.3 (113)	NS <sup>b</sup>
Gonys (cm)	1.27 ± 0.05 (32)	1.25 ± 0.05 (100)	NS
Gape (cm)	5.76 ± 0.19 (32)	5.78 ± 0.21 (100)	NS
Tarsus (cm)	6.23 ± 0.17 (32)	6.20 ± 0.22 (99)	NS
Size <sup>c</sup>	15.7 ± 0.5 (32)	15.8 ± 0.5 (100)	NS
Condition index	4.29 (3)	4.20 (57)	NS

<sup>a</sup> Mean ± SD (sample size).

<sup>b</sup> NS = no significant difference ( $P > 0.05$ ).

<sup>c</sup> Product of discriminant function described in Ryder (1978b).

1871, Verner and Willson 1966, Orians 1969, Selander 1972, Trivers 1972, Emlen and Oring 1977). Females are considered to be the limited resource because they generally are at a reproductive investment disadvantage, contributing a larger energetic input to offspring production (Trivers 1972, Alcock 1975, Wilson 1975, Dawkins 1976, Barash 1977). Monogamy involving male parental care of offspring tends to shift the balance toward equality of investment by the two sexes (Ralls 1977, Wittenberger and Tilson 1980). In such situations some selectivity by males in the mate-selection process should exist (Burley 1977, 1981; Gladstone 1979).

Accepting the hypothesis that female-female pairs are the result of a skewed sex ratio, theory would predict that females would be placed in a position of competition for males (Wilson 1975, Emlen and Oring 1977). It follows that a female able to acquire a male mate under such circumstances may in some way be superior to those that do not succeed. As part of our investigations of the female-female pairing phenomenon in Ring-billed Gulls on Granite Island (48°41'N, 88°29'W), we tested the prediction that individuals involved in this type of bonding were sub-standard birds, i.e. at either extreme of the size range for females, younger, less experienced, or in poorer condition nutritionally or hormonally relative to females of heterosexual pairs.

During the breeding seasons of 1979 and 1980 we trapped 32 females involved in heterosexual pairs and 100 females from homosexual pairs, including 32 pairs, using the drop-trap method (Mills and Ryder 1979). We recaptured 14 of the female-female pair members during the second year of the study. We weighed all trapped birds using a 500- or 1,000-g Pesola hand-held scale (±5 g) and measured gonys, gape, and tarsus (Baldwin et al. 1931) with vernier calipers to the nearest 0.01 cm. Keel length (Harris 1970) was measured, in 1979, to the nearest 0.1 cm. We determined sex by discriminant function (Ryder 1978b); the result of this function was taken as a measure of structural size. A condition index {CI = body weight (g)/[bill length (cm) × keel length (cm)]} for birds trapped in 1979 was calculated following Har-

ris (1970). Ages were determined for birds that had been banded prior to our study.

We collected blood from the brachial artery of 12 females from heterosexual pairs and 27 females from homosexual pairs; time of day and the number of days after clutch completion were controlled. The blood was centrifuged for 20 min at 2,500 rpm within 30 min of collection to separate the blood plasma and to prevent glucose breakdown (Bennett and Bolen 1978). Plasma was extracted, packaged, and frozen in liquid nitrogen. Levels of total estrogens (Hotchkiss et al. 1971), thyroxine ( $T_4$ ; Anon. 1980), corticosterone, progesterone, and total androgens (Abraham 1977) were determined by specific radioimmunoassays.

Alpha-amino nitrogen (following Mathews et al. 1964), urea nitrogen (Urease-Berthelot reaction, Sigma Kit No. 640), uric acid (Sigma Kit No. 680/American Monitor Colorimetric Uricase Uric Acid reagent system No. 1017), total protein (Biuret method of Henry et al. 1974), glucose (American Monitor "Trucose" cat. No. 1054), calcium (American Monitor 60-s calcium cat. No. 1032), and cholesterol (Bio-Rad Quanta-Zyme Triglycerides Kit) were determined colorimetrically. We were unable to do all tests for each bird sampled because of a shortage of plasma.

Statistical analyses followed Nie et al. (1970). We used *t*-tests only with sample sizes greater than 25. When variances were not homogeneous, as determined by *F*-tests, we used separate variance estimates instead of pooled estimates. Mann-Whitney *U*-tests were used when *t*-tests were not appropriate (Siegal 1956).

Females from female-female pairs did not differ significantly from heterosexually paired females in any measure of size, weight, or condition (Table 1). During the study, 14 previously banded females from female-female pairs were trapped. Five had been banded as chicks on Granite Island and hence were of known age. The average age of these birds was  $6.0 \pm 1.9$  yr. The other 9 had been banded as adults; assuming that they developed adult plumage at 3 yr of age, they ranged in age from 4+ to 12+ yr. Females from heterosexual pairs that were banded as

TABLE 2. Blood hormone levels in the plasma of female Ring-billed Gulls from male-female and female-female pairs.

	Male-female pairs	Female-female pairs	
Estrogen (ng/ml)	1.4 ± 0.7 (7) <sup>a</sup>	2.6 ± 2.1 (20)	NS <sup>b</sup>
Androgen (pg/ml)	202 ± 144 (3)	454 ± 242 (10)	NS
Progesterone (ng/ml)	1.6 ± 0.9 (12)	4.8 ± 1.4 (24)	S
Corticosterone (ng/ml)	29.3 ± 9.8 (12)	30.1 ± 10.4 (25)	NS

<sup>a</sup> Mean ± SD (sample size).

<sup>b</sup> S = significant difference ( $P < 0.05$ ), NS = no significant difference.

chicks ( $n = 6$ ) averaged  $6.0 \pm 1.3$  yr of age. Males averaged  $3.8 \pm 1.4$  yr ( $n = 3$ ). Birds have been banded annually on Granite Island since 1971. For birds banded as adults, our age estimates represent minimum ages. In addition to our banded birds, none of the females trapped or observed at superclutches (Kovacs and Ryder 1981, 1983; Kovacs 1982) showed any signs of subadult plumage (see Fox and Boersma 1983). Our results do not support the suggestion by Fox and Boersma (1983) that females involved in homosexual pairs may be young birds.

The only differences in levels of blood-chemistry parameters between females of the two pair types were lower cholesterol and higher progesterone levels in members of female-female pairs (Tables 2, 3). The low cholesterol level is interesting in light of the elevated progesterone levels found for members of female-female pairs because cholesterol serves as a precursor for the synthesis of estrogens (Turner and Bagnara 1976). Progesterone seems to be involved in defeathering of the brood patch (Jones 1971, Farner and Wingfield 1980), and it acts synergistically with estrogen to elicit nest-building and incubation behavior (Cheng and Silver 1975). The elevated levels of progesterone in female-female pairs may be a result of the pair bond and close proximity of the two females, or of a visual or tactile superstimulus provided by their clutches, which contain twice the normal number of eggs. Female mammals living in close proximity have been found to strongly influence each

other's steroid hormone production (McClintock 1981).

The normal level of androgens found in these birds also was reported for female-female pair members in Western Gulls (Wingfield et al. 1980a, b). However, because sample sizes were small and it was difficult to maintain a high level of control in the field, we are unable to draw firm conclusions regarding hormone and metabolite levels from our blood-chemistry work.

Females involved in homosexual bonds were not different from heterosexually paired females in the criteria measured. There are several possible explanations for the limited sex, males, not choosing only the "best" females in our study. First, males in this typically monogamous species, where females usually do the primary choosing, may not be selective beyond some minimum standard. Second, there may not be enough variation among the females that reach breeding condition in a given year to influence a male's fitness. Third, because females in a normally monogamous species do not compete with one another during pair bonding (male-female bonding being somewhat dependent on submissive behavior by females), the exclusion of females from heterosexual bonds may occur on a random basis. Fourth, the year in which a female first breeds may be crucial for life-long mating patterns. Because homosexual pairs of female Ring-billed Gulls exhibit mate fidelity (Kovacs and Ryder 1981), a female mated to another fe-

TABLE 3. Blood metabolite levels in the plasma of female Ring-billed Gulls from male-female and female-female pairs.

	Male-female pairs	Female-female pairs	
Amino nitrogen (mg/100 ml)	5.2 ± 1.8 (12) <sup>a</sup>	5.0 ± 2.1 (27)	NS <sup>b</sup>
Urea (mg/100 ml)	3.7 ± 0.9 (3)	3.4 ± 1.3 (10)	NS
Uric acid (mg/100 ml)	12.6 ± 6.4 (3)	12.4 ± 4.6 (10)	NS
Total protein (g/100 ml)	4.8 ± 0.9 (3)	4.3 ± 0.5 (10)	NS
Glucose (mg/100 ml)	445 ± 18 (3)	408 ± 89 (10)	NS
Calcium (mg/100 ml)	9.8 ± 1.0 (12)	9.8 ± 1.3 (24)	NS
Cholesterol (mg/100 ml)	357 ± 87 (12)	295 ± 31 (24)	S
Triglycerides (mg/100 ml)	165 ± 122 (3)	70 ± 19 (10)	NS
Thyroxine (ng/ml)	22.3 ± 13.3 (12)	16.4 ± 5.0 (27)	NS

<sup>a</sup> Mean ± SD (sample size).

<sup>b</sup> S = significant difference ( $P < 0.05$ ), NS = no significant difference.

male may be unwilling to accept a male mate in preference to her previous partner. Finally, we may not have measured appropriate criteria for mate selection.

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### The Call of Bulwer's Petrel (*Bulweria bulwerii*), and the Relationship Between Intersexual Call Divergence and Aerial Calling in the Nocturnal Procellariiformes

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Breeding colonies of nocturnal petrels are characteristically noisy places, with birds calling from below ground, on the surface, and in flight. The adaptive nature of this vocal activity has been investigated only recently (Brooke 1978; Simons 1981; James 1984a, 1985; James and Robertson 1985a, b). The majority of species exhibit aerial calling, but there are a few notable exceptions. One of these is Bulwer's Petrel (*Bulweria bulwerii*), a little-known species that occurs in the subtropical sectors of both the Pacific and Atlan-

tic oceans (Cramp and Simmons 1977). That it is silent over the breeding colony is beyond doubt (Thibault and Holyoak 1978; Jouanin et al. 1979; James 1984b), despite a mistaken report to the contrary quoted in Cramp and Simmons (1977), which actually refers to the aerial calling of the Little Shearwater (*Puffinus assimilis*; Jouanin et al. 1979). For many of the species examined, a clear sexual dimorphism in voice has been detected (Brooke 1978; Ristow and Wink 1980; James 1984a; James and Robertson 1985a, b), a phenomenon considered to be an adaptation for sexual advertisement in the low light levels in which these birds nest (Brooke 1978). Research has been conducted on only a small proportion of the total

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