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BREEDING BIOLOGY OF THE XANTUS' MURRELET

KELVIN G. MURRAY
KATHY WINNETT-MURRAY
ZOE A. EPPLEY
GEORGE L. HUNT, JR.
AND
DOUGLAS B. SCHWARTZ

ABSTRACT.—Xantus' Murrelets (*Synthliboramphus* [*Endomychura*] *hypoleucus*) were studied on Santa Barbara Island, California from 1975 to 1979. Clutch initiation occurred from March to June and usually peaked in April. The two-egg clutch was 45% of the female's weight. Eggs were laid eight days apart. Both sexes shared duties during a 34-day incubation period; partners relieved one another every three to four days. Eggs were typically left unattended in the interval between laying of successive eggs, immediately after clutch completion, and sporadically during incubation. Breeders and non-breeders of both sexes followed similar patterns of weight change, reflecting similar patterns of colony attendance; murrelets lost weight after the egg-laying period, then gradually gained weight through the rest of the breeding season. The downy young left the nest only two nights after hatching, unfed and weighing less than 30 g. Chicks and their parents apparently moved well offshore their first night at sea. Even though most murrelets on Santa Barbara nested in concealed rock crevices, irregular nest attendance patterns left eggs vulnerable to predation, resulting in the loss of 44% of the eggs laid. Predation by deer mice (*Peromyscus maniculatus*) is currently the greatest risk to the breeding of these murrelets on Santa Barbara Island.

The Family Alcidae is unusual for its diversity of breeding habits and the range of developmental patterns in its young (Sealy 1972, 1973a). Most alcids have semiprecocial young that develop thermoregulatory abilities early, but that remain in the nest until reaching about 90% of adult weight (Sealy 1973a). In contrast, the murrelets of the genus *Synthliboramphus* (now including *Endomychura*; A.O.U. 1982) represent the extreme of precociality; their young go to sea within days of hatching, at about 15% of adult weight. These murrelets are also unusual in that they produce two young and typically forage far from the colony during the breeding season (Sealy 1975a, 1976, Hunt et al. 1979).

Sealy (1972) proposed that in alcids the ecological advantage of taking their young to offshore foraging areas is the primary selective force for precociality. With precocial young able to travel to foraging areas, feeding rates are presumably higher than if adults had to bring food back to the nest (Scott 1973). Murres (*Uria* spp.), which go to sea feathered and at 20% of adult weight, have higher growth rates at sea than when the adults feed them in the nest (Varoujean et al. 1979). Cody (1971, 1973) proposed that precociality is also an adaptation to reduce predation on nestlings. If mortality at sea for young birds under parental care is low, then the two-egg clutch and precocial young of the *Synthliboramphus* murrelets may allow them to rear twice as many young as other seabirds that forage offshore.

This paper presents new information on the breeding biology of Xantus' Murrelets (*S. hypoleucus*). By examining aspects of their life history in relation to hypotheses for the development of precociality in the alcids, we hoped to identify some of the costs and benefits associated with this breeding pattern. Before our study, only anecdotal information on the breeding biology of Xantus' Murrelets was available (Lamb 1909, Howell 1917, Bent 1919). Two other murrelets with similar breeding habits and precocial young have been studied: the Ancient Murrelet (*S. antiquus*; Sealy 1976) and Craveri's Murrelet (*S.* [*Endomychura*] *craveri*; DeWeese and Anderson 1976).

DISTRIBUTION

Xantus' Murrelets nest on offshore islands between central Baja California and Point Conception, California (A.O.U. 1957, Udvardy 1963, Jehl and Bond 1975). On the California Channel Islands only *S. h. scrippsi* breeds regularly (Jehl and Bond 1975, Winnett et al. 1979). Santa Barbara Island is the site of the species' largest breeding colony, which we estimated contained 6,000–10,000 individuals during the breeding seasons 1976–1978. After the breeding season, the birds generally move northward, sometimes well out to sea (Feinstein 1958, Scott et al. 1971, Sanger 1973, Jehl and Bond 1975).

STUDY AREA AND METHODS

Xantus' Murrelets were studied on Santa Barbara Island, California, from 18 April to 30 May 1975 (ZAE, DBS, GLH), 13–22 March (ZAE, DBS) and 4 April to 17 July 1976 (KWM, GLH), 6 March to 7 July 1977 (KGM, KWM), and 22–23 January and 16 March to 29 June 1978 (KGM, KWM). Additional observations were made on visits to the island on 26 March to 2 April, 24 April to 1 May and 29 May to 10 June 1979 (KWM).

Santa Barbara (33°30'N, 119°02'W) is 2.6 km^2 and lies 64 km southwest of Los Angeles and 39 km west of Santa Catalina Island. Its coastline consists of sheer cliffs and a few narrow, rocky beaches. Annual rainfall is about 31 cm with most rain occurring from October to April. The climate is mild but strongly influenced by west-northwest prevailing winds, which average more than 27 km/h at exposed sites and 12.6 km/h at sheltered sites (Philbrick 1972). Further details of the island topography, climate and flora are given in Philbrick (1972).

Howell (1917) and Hunt and Hunt (1974) described the avifauna, including the nine species of seabirds breeding at the time of this study. The terrestrial mammalian fauna consists of an endemic deer mouse (*Peromyscus maniculatus elusus*) and a small population of introduced rabbits (*Oryctolagus cuniculus*). Feral cats, abundant on Santa Barbara in the late 1800's and early 1900's (Howell 1917), were reduced to one survivor by the time our study commenced, and this cat was eliminated by 1978.

Our two main study sites were in relatively accessible areas that contained the greatest concentrations of nesting murrelets. One site included the rocky outcrops near the mouth of Cat Canyon (Fig. 1), including the 45° south-facing slope just west of the canyon proper. Vegetation was sparse, consisting mainly of iceplant (*Mesembryanthemum crystallinum*), cholla (*Opuntia prolifera*), pineapple weed (*Amblyopappus pusillus*) and box thorn (*Lycium californicum*). The second site, on the eastern slope, was between Landing Cove and Cave Canyon on a 45° slope facing east-northeast. The lower part of this slope was dominated by the shrub *Eriophyllum nevinii* growing on a rock substrate; the upper portion consisted of soft soil and was covered with several grasses including bromegrass (*Bromus* spp.), barley (*Hordeum glaucum*) and wild oat (*Avena* spp.).

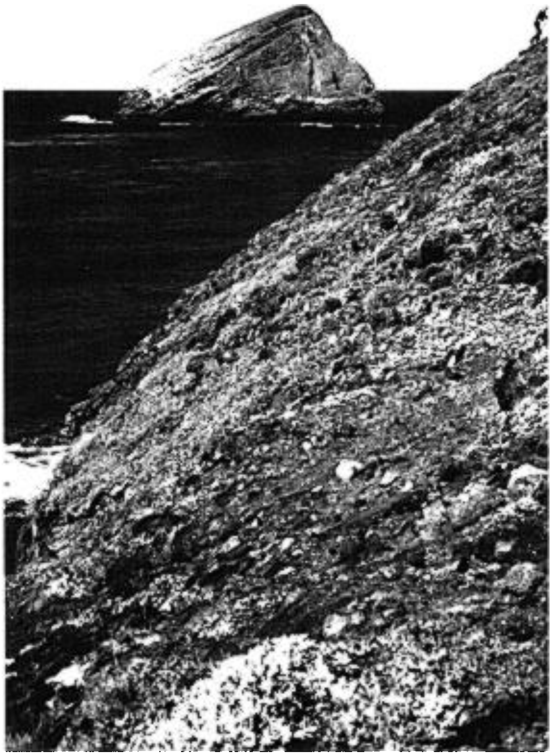

FIGURE 1. The Cat Canyon study area with Sutil Islet in the background, showing the sparsely vegetated cliff slope nesting habitat of Xantus' Murrelet.

Two additional sites were visited less frequently. One, on the east side of the island at the mouth of Cave Canyon, was dominated by *Eriophyllum* growing on rock. The other, West Cliffs, was on the west side of the island at the periphery of the Western Gull (*Larus occidentalis*) colony. A large rock outcrop there provided many nesting sites. The vegetation at this site was sparse, consisting only of low-growing iceplant and fiddleneck (*Amsinckia intermedia*).

We searched all accessible areas each year for murrelet nests. In 1978 we measured distances to nearest conspecific neighbors and to the ocean at all study nests for which we could safely reach the cliff edge and/or nearest neighbor.

Breeding phenology was obtained by visiting nest sites every one or two days. In 1975 we visited only the east slope and Cave Canyon sites regularly. In all other years, previously used nest sites in each study area and all suitable nesting habitat in Cat Canyon and on the east slope were visited at least every other day, usually daily. If nests contained eggs when first found, we estimated the date when clutches were started as either eight days before the laying of the second egg (average time between laying of two eggs) or 43 days before the date of hatching (average time from laying of first egg to hatching). When adults were absent, we marked eggs to denote order of laying, and weighed them. We monitored the internal egg temperature during incubation at two nests in 1978 using the methods of Drent (1967).

We studied nest site attendance by color-marking adults at nests that were being checked daily. Birds were marked with small spots of colored enamel paint on the head or back. Additionally, before and during the egg-laying periods of 1977 and 1978 we visited several nests on the eastern slope nightly to determine patterns of nocturnal nest visitation.

Incubating murrelets almost invariably flew from nests when touched. Flushed incubators often remained absent for several days. Therefore, after 1975 we restricted handling of incubators to the individual marking of about 20 birds. Also after 1975, no incubators at the Cave Canyon and West Cliffs sites were marked. Since brooding adults were much less prone to desert chicks, these adults were banded the day before we expected their chicks to depart to sea.

In 1977 and 1978 other adults were captured and banded at night (between 20:00 and 06:00 in mist-nets set up near breeding colonies at seven locations on the island periphery; the same sites were used in both years. We recorded each bird's weight, breeding status, capture time, and flight direction (i.e., arriving or departing island). Weights of egg-bearing females were recorded as total weight minus 37 g, the average weight of a fresh murrelet egg in 1977 and 1978.

To study seasonal weight change in the murrelets, we needed to distinguish between the sexes and between breeding and non-breeding birds. We identified breeding birds by their brood patches and the presence of eggs in females. We assigned non-breeding status to birds without brood patches that were captured at least twice between the late egg-laying and peak hatching periods (15 April–10 June 1977 and 11 May–22 June 1978). Birds that were captured once during these periods, and lacked brood patches, or were captured outside of the designated period, were considered of unknown breeding status; their weights were not used in the analysis. By this criterion, "non-breeders" included both subadults that had never bred and adults that may have bred previously, but not in the year of capture. We were able to distinguish between novice and experienced non-breeding birds in only a few instances involving banded individuals.

Murrelets carrying eggs were identified as females; their partners were assumed to be males. Another eight murrelets, four of each sex, were sexed by laparotomy in 1978. The incision was 2 cm or less, and the skin was closed with Super Glue to prevent water from entering the body. Two murrelets that were recaptured a month after the operation showed only a small amount of scar tissue.

RESULTS

SEASONAL COLONY ATTENDANCE

Xantus' Murrelets began arriving in small numbers near Santa Barbara Island in January, but we did not see them on the island until March when breeding commenced. Murrelets visited potential nesting sites irregularly, and as early as two months before laying eggs, but typically their nocturnal visits to nests began two to three weeks before egg-laying. In June, adults with newly hatched young dispersed rapidly and were rarely seen near the island. By July murrelets were uncommon on or near the island.

BODY WEIGHTS DURING THE BREEDING SEASON

The body weights of adult Xantus' Murrelets changed throughout the breeding season. Adults of both sexes arrived on the island slightly below their maximum summer weight (Fig. 2). They reached their maximum weight during egg laying, then lost 4 to 5% during incubation. They regained this weight during late incubation. The average body weight for adults was 167.0 ± 0.67 g (375), range = 136–215 g. Breeding murrelets (171.0 ± 0.67 g [171]) were not significantly heavier than non-breeding murrelets [163.5 ± 0.77 g (191)] (t [360] = 0.762, $P > 0.4$). These murrelets are not sexually dimorphic (Jehl and Bond 1975), but we found females were heavier than their male companions in both breeding pairs (11-g difference, $t = 2.88$, $P < 0.01$, $n = 13$) and non-breeding pairs (26.5-g difference, $t = 2.16$, $P < 0.05$, $n = 4$) (Fig. 3), using paired comparisons. Changes in weight associated with nest attendance were also found and will be discussed in the section on incubation.

CIRCADIAN ACTIVITY

Xantus' Murrelets are nocturnal, limiting all land-based activities except incubation to hours of darkness. After dusk and before dawn, murrelets congregated on the waters below the densest nesting areas. Censuses conducted by boat just before dawn indicated that birds were most numerous in these staging areas in mid-May, coincident with the hatching period. Murrelets began flying ashore immediately after dark each night. Two peaks of activity were evident, one 2 to 3 h after dark (22:00–24:00)

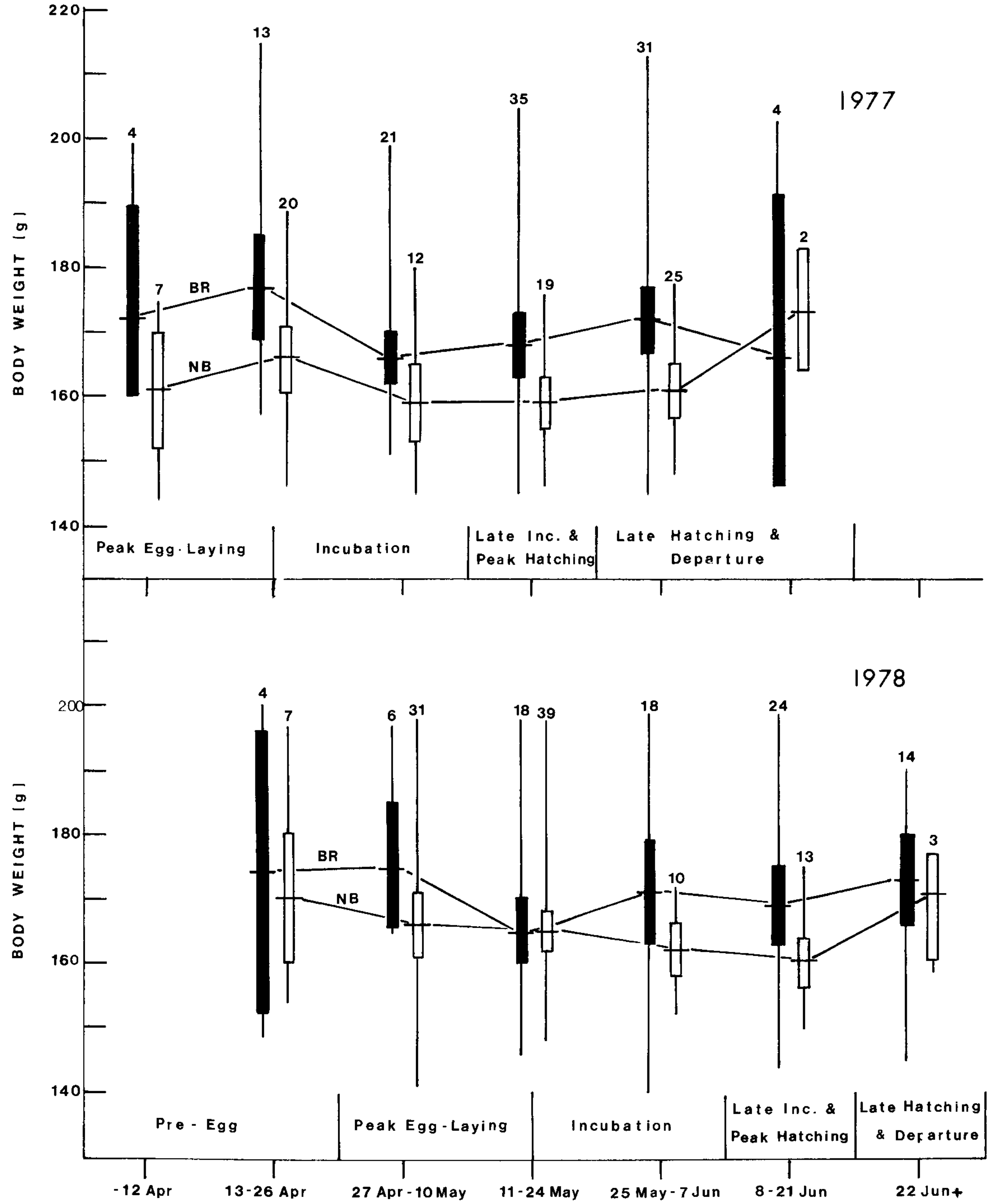

FIGURE 2. Weight changes and timing of reproductive events in Xantus' Murrelets on Santa Barbara Island during the 1977 and 1978 breeding seasons. Horizontal lines denote the mean weights for each time period, vertical lines indicate range, and bars denote twice the standard error on each side of the mean. Solid bars indicate breeders and open bars denote non-breeders. Sample size is given above each line.

and another just before dawn (05:00), when birds left the nesting areas and went to sea.

NESTING DISPERSION AND COLONY STRUCTURE

Unlike many alcids, Xantus' Murrelets tend to nest in small colonies. On Santa Barbara Island, their nests were clumped, probably due to the patchy distribution of suitable nesting habitat. Nearest-neighbor distances ranged from 0.15 to 40 m, and averaged 5 m (n = 172).

These birds usually retained the same nest site and mate in successive breeding seasons. Out of five pairs banded at their nests in 1977 and 1978, three stayed together and main-

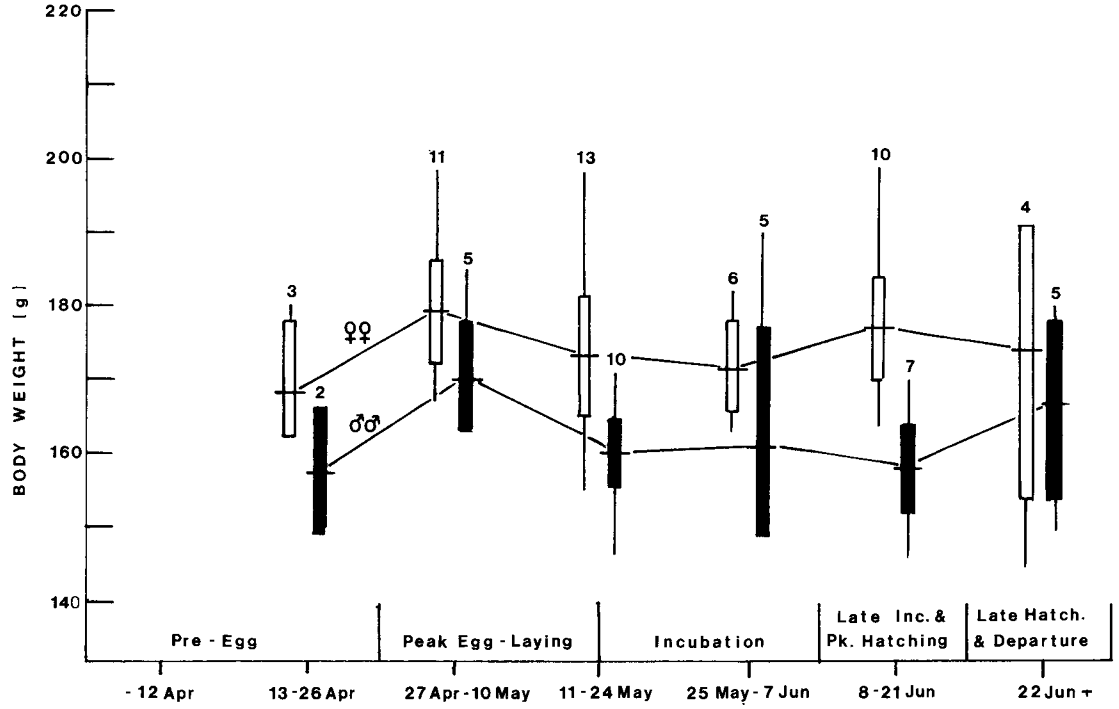

FIGURE 3. Weight changes in breeding and non-breeding male and female Xantus' Murrelets during the 1978 breeding season. Horizontal lines denote mean weights for each time period, vertical lines indicate range, and bars denote twice the standard error on each side of the mean. Weights of egg-laying females are minus the fully shelled egg. Sample size is given above each line.

tained the same nest site in both years. Of 20 individuals banded at their nests, 13 maintained the same nest for three consecutive years, four maintained the same site for four consecutive years, and another moved its nest 0.5 m from the original site, but remained under the same bush. In four cases, banded murrelets abandoned their nests; these sites were not used by murrelets in the following year. One banded murrelet, known to have nested in 1977 but not in 1978, visited its 1977 nest site repeatedly during 1978. We often found single and paired murrelets repeatedly occupying the same sites at night throughout the breeding season, although they never laid eggs.

THE NEST

Xantus' Murrelets nested in rock crevices or under other forms of cover in all areas around the periphery of Santa Barbara Island and on nearby Sutil Islet. Nests were within 150 m of the cliffs, between 3 to 133 m above mean high tide level. The average distance from the nest to the cliff edge was 24.9 ± 1.6 m (120). Concentrations of nests were greatest at the lower ends of canyons with exposed rocky ground.

Seventy percent of the sites used at least once during our study ($n = 244$) were in rock crevices, which provided protection against insolation and avian predators. However, other available habitat that provided shelter and concealment was also used, including *Eriophyllum* (21%) and other plants (6%), rabbit and Burrowing Owl (*Athene cunicularia*) burrows (3%), and man-made structures (a quonset hut, its adjacent shed and boxes, 2%). We found no evidence of nest construction or burrowing. Eggs were laid either on bare rock or in a shallow depression in nests with soft substrates. In some nests dried iceplant accumulated, apparently the cache of deer mice.

EGG AND CLUTCH SIZE

The eggs of these murrelets are among the largest, relative to adult body weight, in the Alcidae (Sealy 1975b). The mean weight of 100 freshly laid eggs was 37.2 ± 2.87 g, range 29.5–43.5 g, or 22.3% of the average adult body weight. The second egg of the clutch averaged over 1 g heavier than the first (37.9 ± 0.62 g [28] vs. 36.6 ± 0.44 g, $t\,[27] = 2.44$, $P < 0.05$). The average time between the laying of the first and second eggs was 8 ± 0.82 days (42), which is longer than the interval reported by Howell (1917) and Bent (1919). The distribution, in days, of laying intervals was as follows: 5 (2), 6 (1), 7 (2), 8 (25), 9 (10), 10 (1), 12 (1). The first egg was unattended until after the second egg was laid, at least during daylight hours.

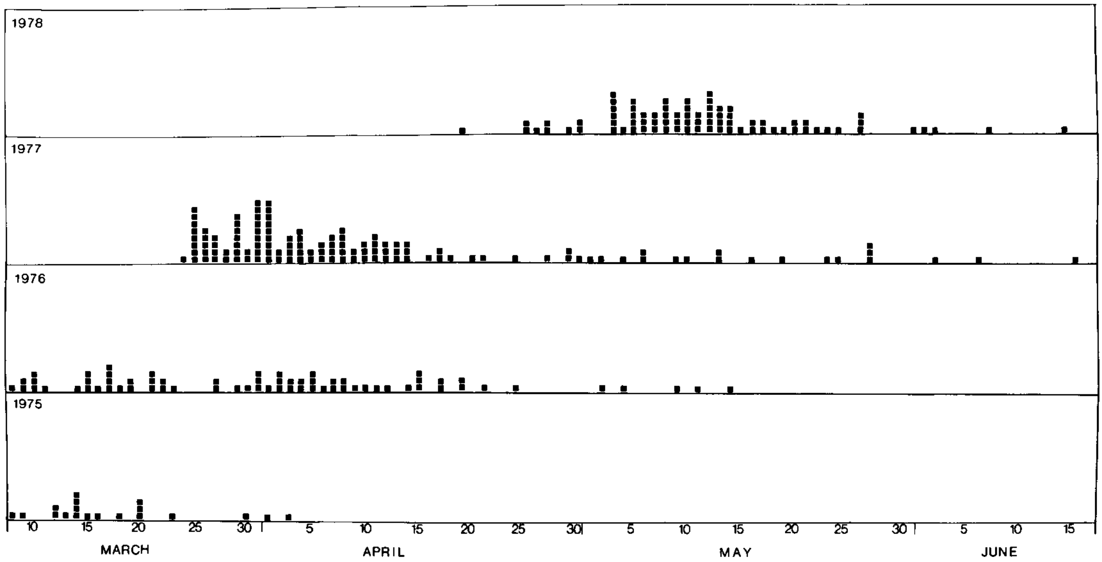

FIGURE 4. Timing of clutch initiation in Xantus' Murrelet during the 1975–1978 breeding seasons; each square denotes the start of one clutch. Sample sizes are: 19 (1975), 67 (1976), 120 (1977) and 79 (1978).

The clutch typically consists of two eggs; only 25% of 296 nests we examined contained single eggs. Fifteen nests contained three eggs and two nests contained four eggs. However, we were not able to prove that these clutches represented the efforts of a single female.

Xantus' Murrelets on Santa Barbara Island began laying eggs in March in all years except 1978. Usually, egg-laying peaked in April and declined sharply through May and June (Fig. 4). In 1978, peak laying was delayed until May. Laying synchrony was estimated in 1976–1978 as the spread of laying dates for the 80% of clutches falling closest to the mean laying date (Coulson and White 1960, Manuwal 1979). Laying synchrony varied among years, from 24 days (1978) to 36 days (1976) and 47 days (1977).

EGG LOSS AND REPLACEMENT

Deer mice preyed heavily on unattended murrelet eggs (Fig. 5). Of 470 eggs laid between 1976 and 1978, 28% were lost to mice before clutch completion and another 16% were lost to mice after clutch completion (at least 8% of these were associated with human disturbance of adults). Other causes of egg loss were minor, but included abandonment either before or after incubation had started (10%, 4%) and accidents (3%), such as rock slides. Only 5% of the eggs incubated to the full term failed to hatch.

The incidence of egg predation by mice differed among study sites and years. Proportionately more eggs were eaten at rocky, sparsely-vegetated areas (Cat Canyon, 46% in 1977, 49% in 1978) than on the grass- and shrub-covered east slope (23% in 1977 and 4% in 1978). This variation may reflect differences in the abundance of other foods used by mice at particular sites or among years (Murray 1980). The most concealing types of nesting habitat did not offer better protection from egg predators; more egg predation occurred among nests in rock crevices or dirt burrows (50%) than in other nesting habitats (38%) ($t = 2.41$, $P < 0.05$).

Lost eggs normally were not replaced. However, at least one pair of color-marked murrelets laid two separate clutches. They laid their first clutch in early April and abandoned it in late May, when the eggs were overdue to hatch. Twenty days later, they started a second clutch. Other nest sites also received second clutches after the first clutch had been destroyed, and we suspect that some of these may be replacement clutches. We have no evidence to support Bent's (1919) claim that murrelets can raise more than one brood in a single season.

BROOD PATCHES

Between the laying of the first and second eggs, Xantus' Murrelets develop a pair of lateral brood patches. Refeathering sometimes began during the last few days on the nest; 20% of the brooding adults ($n = 57$) examined had new pin and ensheathed contour feathers on the brood patch.

INCUBATION

Murrelets were absent from their nest sites, at least during the day, for several days before each egg was laid. On nights when eggs were laid, both members of the pair usually attend-

FIGURE 5. A Xantus' Murrelet egg destroyed by deer mice.

FIGURE 6. The two-day old young of Xantus' Murrelet.

ed the nest. Males usually started incubation (9 out of 11 cases). On average 2 ± 0.4 days (51) elapsed between clutch completion and incubation, but in 25% of the nests, 3–16 days elapsed.

The incubation shifts of Xantus' Murrelet are among the longest recorded among the alcids. Shifts averaged three days; the distribution of incubation shifts was one (50), two (85), three (135), four (113), five (20), and six days (5). Males and females shared incubation equally, both in duration of shifts ($t[59] = 0.703$, $P > 0.05$) and in total incubation time ($t[189] = 0.665$, $P > 0.05$). Incubation was often sporadic, especially during its early stages. Consequently, eggs were frequently unattended. Of undisturbed nests ($n = 117$), 62% were unattended for at least one day during the incubation period (range 0–19 days; Murray et al. 1980). This egg neglect presumably results from the incubating bird's departure to feed before its partner returns.

Egg neglect increased the total length of the incubation period ($r = 0.955$, $P < 0.01$, $n = 37$; Murray et al. 1980). The incubation period averaged 33.6 ± 0.57 days (37), range 27–44 days, although the actual number of days eggs were incubated was less, averaging 30.6 ± 0.40 days (37), range 24–34 days. First eggs hatched an average of 43 ± 0.83 days (20) after laying; second eggs hatched an average of 35 ± 0.70 days (20) after laying.

Weight changes of adults were associated with the long incubation shifts. Breeders captured on incoming flights to the island [172.1 ± 2.0 g (60)] were significantly heavier than those captured on outgoing flights [161.8 ± 1.8 g (39)] ($t = 3.64$, $P < 0.01$). Individual murrelets, captured on successive flights to and from their nests, showed the same pattern of weight change. Five birds weighed before and after an incubation bout lost an average of 4.0 g or 2.2% of their starting weight, per day (range 0.8–8.25 g/day). Four murrelets weighed before and after a foraging trip gained an average of 4.3 g, or 2.7% of their initial weight per day (range 0.75–7.0 g/day).

CHICK STAGE

Chicks hatched between early April and early July. The peak of hatching varied as much as two months among years, ranging from late April to late June. During hatching, the frequency of nest relief increased. Often both adults attended the nest at night. Presumably, these changes enhanced coordination between adults and chicks as the family prepared to go to sea. We found a prolonged period of hatching in Xantus' Murrelets, similar to that found in Ancient Murrelets (Sealy 1976). Cracking of the egg was evident two to five days prior to hatching. We heard chicks vocalizing coincident with the initial shell cracks. The eggs usually hatched within a few hours of each other, but occasionally up to 24 h elapsed between hatching of siblings. In some cases, the second egg laid hatched first. We believe the long hatching period and vocalizations of pipping eggs may be important in synchronizing hatching of the chicks (see Vince 1969, 1970, Orcutt 1974, Brown 1976).

Newly hatched young were downy and had the black-dorsal, white-ventral coloration of the adults (Fig. 6). Juvenal flight and contour feathers were not evident before the chicks departed, and the egg tooth was still present. Newly hatched chicks had feet and metatarsi similar in size to the adults. Although the one- or two-day old chicks were only 15% (24.4 g, $n = 74$) of adult weight, their metatarsi (2.27 cm, $n = 35$) were 98% of adult metatarsal length (2.31 cm, $n = 19$).

Xantus' Murrelet chicks were not fed before departure. They lost an average of 8% of their body weight/day during their stay in the nest.

Day-old chicks (0–24 h) were significantly heavier than chicks ready to depart (25.8 g $n = 22$ vs. 23.8 g $n = 26$, $t[46] = 3.089$, $P < 0.01$).

INCUBATION TEMPERATURES AND THERMOREGULATION

Brood patch temperatures and body temperatures of three incubating murrelets averaged 39.8°C and 41.5°C, respectively. The internal temperature of an egg incubated for 13 days was 34.3 ± 0.19°C (18) and of an egg incubated 19 days was 34.4 ± 0.11°C (18). These temperatures are similar to those summarized by Drent (1967) for the brood patch/egg surface interface of other temperate-nesting seabirds.

The cloacal temperatures of one-to-two-day old murrelet chicks averaged 38.0°C (11) at ambient temperatures of 19–21°C; this is within 3°C of adult temperature. Sealy (1976) found that young Ancient Murrelets can maintain nearly adult body temperatures at two days, even when exposed to 8.9–11.2°C.

DEPARTURE

Chicks typically departed the island one to two days after hatching; if there were two chicks in a nest, they usually left together on the night after the second egg hatched. In a few unusual cases, chicks spent three to five days in the nest. Departures occurred exclusively at night, presumably reducing potential predation by gulls. However, one family departed before dusk shortly after they were disturbed by research activity.

Chicks were normally escorted from the nest by both parents on the night of departure. Following a period of intense vocalizations, the family emerged from the nest together. Parents typically led the chicks down the slope for less than 2 m before flying out to sea. Left on their own, the chicks made their way directly to the cliff edge where they jumped or were blown off the cliff into the surf 75 m or more below. The chicks may have been guided to sea by calls from their parents or other murrelets. We were unable to observe a reunion at sea.

As with Ancient Murrelets (Sealy 1976, Sealy and Campbell 1979), family groups of Xantus' Murrelets probably move far offshore during their first night at sea. Although the downy chicks cannot fly, they are accomplished surface swimmers and divers, using their wings for propulsion under water (Howell 1917; B. Burgeson and P. Kelly, pers. comm.).

Despite an extensive at-sea census program in 1975–1977, we rarely encountered murrelet chicks at sea. Of five sightings, all were chicks in the presence of two adults. Three of these groups were encountered more than 18.5 km from Santa Barbara Island (Hunt et al., unpubl. data). DeWeese and Anderson (1976), observing family groups of Craveri's Murrelets at sea, felt that the adults and young foraged as a unit. They also saw adults passing small fish to the chicks.

PREDATION ON ADULTS AND CHICKS

The major predator of adult murrelets on Santa Barbara Island is the Barn Owl (*Tyto alba*). At least two Barn Owls were present during this study. We found the sterna from at least 109 Xantus' Murrelets and Cassin's Auklets (*Ptychoramphus aleuticus*) at a roosting cave that was used by Barn Owls for at least three years. Although Western Gulls may sometimes kill adult murrelets (Oades 1974) and Cassin's Auklets (Manuwal 1979), they probably have little effect on the murrelets of Santa Barbara Island. We found no evidence for gull predation on adult murrelets during a concurrent study of Western Gull diets on Santa Barbara. Peregrine Falcons (*Falco peregrinus*) and feral cats were probably important predators on Santa Barbara Island in the past.

Chick mortality on the island was low. Mouse predation on unattended chicks (two chicks), or hatching eggs (five chicks) was the largest cause of chick loss. Western Gulls may take a few Xantus' Murrelet chicks at sea or as they leave the nest; we found three regurgitated carcasses of murrelet chicks at Western Gull nests.

DISCUSSION

This study is the first extensive report on Xantus' Murrelet breeding biology. We found many similarities between the reproductive biology of Xantus' Murrelets and that of Ancient Murrelets (Sealy 1972, 1976), despite their different physical environments. These two species nest at opposite ends of the latitudinal range of the murrelets (Udvardy 1963). They experience different temperature and light cycles, nest in different-sized colonies, and appear to feed at different trophic levels (Sealy 1975a, Hunt et al. 1979). Both species are nocturnal in their activities on land, have two large eggs, share similar patterns of nest attendance, and have precocial young. Craveri's Murrelets also lay two large eggs and have precocial young (DeWeese and Anderson 1976).

Precociality allows parents to increase their actual foraging time (Sealy 1972, 1973a, Scott 1973), yet it also limits nest attendance patterns. First, because large eggs are required to produce chicks that hatch at an advanced developmental stage, females apparently must forage for several days before laying each egg. Second, synchronous hatching is necessary if both chicks are to depart together. Incubation, which presumably could be initiated by males at the time the first egg is laid, is delayed until clutch completion, apparently to prevent asynchronous hatching. Behavioral mechanisms such as increased frequency of incubation shifts at the time of hatching, the extended hatching period, and vocalizations from chicks in pipping eggs may also ensure synchrony of hatching. The result of these constraints is that first-laid eggs are left unattended for several days.

Xantus' Murrelets leave eggs unattended during incubation as well. Egg neglect similar to that found in Xantus' Murrelets has been reported previously only in procellariiforms that travel long distances for patchily distributed food (see Boersma and Wheelwright 1979), although Sealy's (1976) diagram of the sporadic incubation patterns of Ancient Murrelets indicates that egg neglect occurs in this species also. The incidence of egg neglect in Xantus' Murrelets was greatest early in incubation, when over 40% of the nests were unattended at least one day during the first five. Neglect generally decreased throughout incubation, until the length of a normal incubation period had elapsed (Murray et al. 1980). Weights of both Xantus' and Ancient murrelets dropped soon after egg-laying, then gradually increased during the latter part of incubation (Sealy 1976, this study). Our data indicate how this overall weight gain was accomplished in Xantus' Murrelets; individuals gained more while foraging than they lost while incubating. These changes, and the observation that murrelets delay incubation for the first few days after clutch completion, suggest that it is important for murrelets to spend time foraging after egg-laying. Many other seabirds lose weight following egg-laying, which has been interpreted as an indication of energetic stress during that period (Richdale 1947, Harris 1966, Bedard 1967, Fisher 1967, Sealy 1973b, 1976, Ainley et al. 1974, Boersma and Wheelwright 1979).

Because the number of days spent incubating was inversely proportional to the number of days eggs were left unattended, egg neglect actually reduced the number of days that eggs had to be incubated. Thus, murrelets may gain a savings in total incubation time by leaving their eggs unattended during periods when it is advantageous to invest this time in foraging.

On the other hand, leaving eggs unattended has important negative consequences to Xantus' Murrelets. Unattended eggs are often eaten by mice, accounting for 44% of all egg mortality; overall hatching success was only 39%. Mice also ate unattended chicks. On Santa Barbara then, severe mortality at murrelet nests seems to be a direct result of the sporadic incubation patterns associated with the production of two precocial offspring. Cody (1971, 1973) suggested that severe predation pressure, especially on the young, could lead to the development of precociality by rendering early nest departure advantageous. He reasoned that exposed nest sites should be vacated earlier, but Sealy (1973a) pointed out that the precocial young of *Endomychura* and *Synthliboramphus* leave well-concealed crevices or burrows at two days of age. Whereas the concealed rock crevices used by Xantus' Murrelets on Santa Barbara gave little protection from mice, they may have been more effective against most avian and larger mammalian predators.

If predation is severe, why don't murrelets raise only one, well-attended chick? Further work will be necessary to determine if the benefits gained by occasionally raising two offspring outweigh the cost of losing eggs in some years. A small part of this cost may be offset through lower investment in first-laid eggs, which weigh less and are more likely to be eaten, than second-laid eggs.

Alternatively, deer mice may have been less important predators on murrelet eggs in the past. We have no historical information on mouse populations on Santa Barbara, but the grasses that now cover much of the island were introduced during this century (Philbrick 1972). The introduction of these grains (*Bromus, Hordeum* and *Avena* spp.), the seeds of which comprise an important food of mice on Santa Barbara (Murray 1980), could have led to a recent increase in the mouse population. If so, the cost of irregular nest attendance patterns in Xantus' Murrelets on Santa Barbara may be much greater now than it was in the past.

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Department of Biology, California State University, Northridge, California 91330. Present address of first and second authors: Department of Zoology, University of Florida, Gainesville, Florida 32611. Address of third through fifth authors: Department of Ecology and Evolutionary Biology, University of California, Irvine, California 92717. Received 6 August 1981. Final acceptance 25 September 1982.