# MOONLIGHT AVOIDANCE BEHAVIOR IN LEACH'S STORM-PETRELS AS A DEFENSE AGAINST SLATY-BACKED GULLS

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ABSTRACT.—Diurnal activity patterns of Leach's Storm-Petrels (Oceanodroma leucorhoa) and Slaty-backed Gulls (Larus schistisagus) were investigated. The petrels reduced activity in moonlight in May and June when the predation rate by gulls was relatively high. Petrel activity levels were inversely correlated with light intensities and the corresponding risk of predation by the gull. This suggests that nocturnal activity and moonlight avoidance by the petrel in its colony are an effective defense against diurnal predators. Activity synchronization of the petrel was most marked during the full moon, further supporting the predatoravoidance hypothesis. Received 15 October 1984, accepted 27 April 1985.

MANX Shearwater (Puffinus puffinus; Harris 1966), Leach's Storm-Petrel (Oceanodroma leucorhoa; Harris 1974), Fork-tailed Storm-Petrel (O. furcata; Harris 1974, Boersma et al. 1980), and Cassin's Auklet (Ptychoramphus aleuticus; Thoresen 1964, Manuwal 1974) are strictly nocturnal in their colonies and are less active on moonlit nights than on dark nights. Cody (1973) discussed the nocturnal activity of alcids as a defense against diurnal predators. Gross (1935), M. P. Harris (1966), and S. W. Harris (1974) also suggested that nocturnal procellariiforms are vulnerable to diurnal predatory gulls on moonlit nights. However, the relationship between daily activities of procellariiforms and predation risk has not been studied.

I studied Leach's Storm-Petrels and Slatybacked Gulls (*Larus schistisagus*) on Daikoku Island. Their activity patterns are described and the nocturnal behavior of the petrels in the colony is discussed as predator avoidance.

#### STUDY AREA AND METHODS

The colony.—The study was conducted on Daikoku Island (42°52'N, 144°52'E), Akkeshi, Hokkaido, between late April and early October 1982. The island is 6.1 km in circumference and treeless, with the exception of birch (*Betula ermanii*) groves in the ravines. Leach's Storm-Petrel (the only petrel breeding on the island) nests in the interior parts of the island, which is covered with Artemisa montana and Urtica platyphilla. Abe et al. (1972) estimated that there were 1,070,000 breeding pairs of petrels, but a more recent estimate is 415,000 (Watanuki 1985b). About 3,500 pairs of Slaty-backed Gulls nested on maritime slopes, which are covered with *Calamagrostis langsdorffii*, isolated rock stacks, and cliff ledges. A few pairs of Blacktailed Gulls (*L. crassirostris*) nested on these sites.

The Slaty-backed Gull is an important predator of adult petrels on the island. Although Jungle Crows (*Corvus macrorhynchos*) excavated petrel burrows and ate adults, eggs, and chicks, predation by the small crow population (13 pairs) was not significant.

Activity patterns.-Observations of flying birds were made from a blind set on top of a headland about 25 m above sea level. For 5 min every 30 min, I counted all birds passing an imaginary 20 × 30-m plane oriented vertically with reference to the cliff face opposite the headland. Two 6-volt electric lights, one set horizontally and the other about 45° upward at the blind, lit the plane facing toward the sea from the lower corner to the opposite side. This reduced the effect of the light on landing birds approaching from the sea. If all the landing petrels were attracted instantaneously to the lights, the number of petrels flying through the lights would increase during the observations. However, the number was rather constant during 5-min observations (Fig. 1). A few petrels and gulls flew circularly in the lights; these were excluded from the data. Observations on moonlit nights showed that Slaty-backed Gulls did not avoid the lights. No differential response to the lights by gulls and petrels was assumed. Observations started in daylight and lasted 24 h (n = 19 days). Data taken during a day with dense fog (13-14 May) were excluded from the analysis because of low visibility. Data of 27-28 April were included in those of May.

Light intensity was measured by a lux-meter ( $\pm 10\%$ ) set horizontally and was divided into four classes: dark (0 1ux), moonlight with no cloud cover (<1 lux), twilight (1-5 × 10<sup>4</sup> lux), and daylight (>5 × 10<sup>4</sup> lux). Time of sunrise, sunset, moonrise, and moonset were from the astronomical tables for Kushiro, about 40 km west of Daikoku Island.



Time after lighting (min.)

Fig. 1. Number of flying Leach's Storm-Petrels per 30 s in relation to time after lighting by two 6-volt lights, one set horizontally and the other about 45° upward. The 5-min experiment was repeated three times.

Overlap of petrel and gull activity was assessed by Pianka's overlap index (Pianka 1973):

$$O_{xy} = \sum x_i y_i / (\sum x_i^2 \sum y_i^2)^{\aleph},$$

where  $x_i$  = the number of petrels flying per 5 min and  $y_i$  = the number of gulls flying per 5 min. The time dispersion of petrel activity between 1930 and 0230 was determined by Morishita's I $\delta$  index (Morishita 1959):

$$\mathbf{I}\delta = K[\Sigma x_i(x_i-1)]/\Sigma x_i(\Sigma x_i-1),$$

where  $x_i$  = the number of petrels flying per 5 min and K = the number of samplings (K = 15 in this case).

Predation by gulls.—I estimated the number of Leach's Storm-Petrels eaten by Slaty-backed Gulls from the energy requirements of gulls and their food composition. The food habits of the gulls were determined by collecting pellets and food remains at their nesting sites. During the study, collections were made every 5 days in 4 study quadrats with a total of 114 nests, yielding 1,143 samples. The energy requirements of Slaty-backed Gulls were estimated by using a simple modification of the model of Furness (1978). Calculations of energy requirements and food composition of the gulls are shown in Appendices 1 and 2. The number of petrels killed was calculated for 5-day periods and was combined monthly.

Petrel breeding.—Ten  $4 \times 10$ -m study quadrats containing a total of 351 active petrel burrows were used. I checked the nests every 5 days and recorded the contents. Twenty-five pairs incubating eggs were

TABLE 1. Breeding schedule of the petrel and its nest duties shown by egg-days and chick-days in the study plots.

	May	June	July	Aug	Sept
No. of eggs laid No. of chicks	0	335	16	0	0
hatched	0	0	199	64	0
Egg-days	0	5,785	6,305	390	0
Chick-days	0	0	1,965	7,220	6,935

marked by individually numbered rings. Their nests were checked every day between 4 and 9 July to determine the length of incubation stints. I estimated chick feeding frequency by weighing 15 chicks at 0900 and 2100 on 9 August, and at 0300 and 1500 on 10 August. A feeding was assumed to have occurred when a chick gained weight during this interval. This is a minimum estimate since more than one feeding may occur in the interval. Night nest attendance in the prelaying period was estimated by checking if toothpicks placed at the entrance of the active burrows the previous day were moved.

The significance of the correlation coefficient (r)and the difference between values was examined by ANOVA (Sokal and Rohlf 1969).

#### RESULTS

Breeding of petrels.—Petrels arrived in late April and laid eggs between early June and early July. Chicks hatched between mid-July and mid-August and fledged between late September and mid-October. The incubation duty as shown by egg-days was high in June and July, and the chick feeding duty shown by chick-days was high in August and September (Table 1).

Breeding Leach's Storm-Petrels visited their nests 0.6 times/night (a total of 63 nests visited out of 105 nests checked) in the prelaying period, fed a chick at least 1.2 times/night (n = 15), and exchanged incubation duties at 2.9 days (n = 17) on the average. These figures agree with those of other observers (Gross 1935, Wilbur 1969).

Light intensity and activities.—Leach's Storm-Petrels arrived at Daikoku Island about 1 h after sunset and left 1–2 h before sunrise (Fig. 2). The mean number of flying petrels and gulls was related to light intensity (Fig. 3). Petrels were nocturnal and rarely flew in twilight or daylight on the island. More petrels flew in darkness than in moonlight in May ( $F_{1.64} = 6.50$ , P < 0.05) and June ( $F_{1.42} = 7.79$ , P < 0.01); re-



Time of day (hrs)

Fig. 2. Daily changes in the number of flying petrels (dark lines) and gulls (light lines) per 5 min. Heavily shaded areas represent dark times, and lightly shaded areas represent moonlight times. Vertical lines indicate sunrise and sunset.

duced activity in moonlight also occurred in July, although the difference was not significant ( $F_{1.56} = 3.26$ , NS). Petrels did not avoid moonlight in August ( $F_{1.46} = 0.30$ , NS) and September ( $F_{1.72} = 3.51$ , NS). The mean number of petrels flying at each light intensity was negatively correlated with that of the gulls (r = -0.662, n = 20,  $F_{1.18} = 14.4$ , P < 0.01; Fig. 3).

Slaty-backed Gulls rarely flew in the dark (Figs. 2, 3). More gulls flew in moonlight than in darkness in all the months (May:  $F_{1,64} = 56.13$ , P < 0.01; June:  $F_{1,42} = 12.33$ , P < 0.01; July:  $F_{1,56} = 25.3$ , P < 0.01; August:  $F_{1,46} = 5.13$ , P < 0.05; September:  $F_{1,72} = 4.09$ , P < 0.05). Gull activity levels were higher in twilight than in moonlight in all months (May:  $F_{1,75} = 26.96$ , P < 0.01; June:  $F_{1,59} = 36.15$ , P < 0.01; July:  $F_{1,65} = 81.96$ , P < 0.01; August:  $F_{1,55} = 79.12$ , P < 0.01; September:  $F_{1,70} = 168.71$ , P < 0.01) and higher in twilight than in daylight in May ( $F_{1,123} = 34.62$ , P < 0.01) and June ( $F_{1,98} = 11.96$ , P < 0.01).

I observed Leach's Storm-Petrels flying in daylight 11 times. Six of these petrels were

killed immediately by Slaty-backed Gulls and 1 by Jungle Crows. This suggests that there is considerable potential predation risk in twilight and daylight hours.

The time overlap of petrel and gull activity, shown by  $\ln Oxy$ , was positively correlated with the length of the period of moonlight (h; r =0.812, n = 15,  $F_{1,13} = 21.29$ , P < 0.01; Fig. 4) when the data of the days with no overlap (i.e. Oxy = 0) were excluded. Encounter-rate indices (number of petrels × number of gulls) were calculated directly from Fig. 3 and were in the order moonlight > dark > twilight > daylight. I do not have direct evidence of predation under moonlight, although the indirect evidence above corroborates Gross's (1935) finding that most encounters between gulls and petrels occur during moonlight.

Activity patterns of petrels.—Most petrel activity occurred at about 2400 or between 2200 and 0100 on nights with a new moon, 0130 on nights with a full moon, 2200 on nights with a halfmoon rising at midnight, and 0100 on nights with a half-moon setting at midnight (Fig. 2),



Fig. 3. Mean number of flying petrels (shaded bars) and gulls (open bars) per 5 min under dark (D), moonlight (M), twilight (T), and daylight (DL) conditions. Sample sizes of gulls and petrels are the same and are shown above the bars.

as has been reported in Cassin's Auklet (Manuwal 1974) and in Leach's Storm-Petrel in California (Harris 1974). The petrels on Daikoku Island arrived later on full-moon nights (5-6 May, 5-6 June, and 5-6 August) and earlier on nights when the half-moon rose at midnight (10-11 June, 8-9 July, and 11-12 August) than they did on nights without a moon (27-28 April, 23-24 May, 19-20 July, and 15-16 August; Fig. 2).

On nights in May, June, and July with quarter or half-moons, the mean number of petrels flying per 5 min during darkness ( $\bar{x} = 155.6$ , n = 42) was significantly higher than that ( $\bar{x} =$ 100.0, n = 30) on moonless nights in the same months ( $F_{1.30} = 37.47$ , P < 0.01). The petrels, therefore, seemed to anticipate the lunar cycle and synchronize their activity to the hours of darkness on clear nights with a half-moon,



Fig. 4. The correlation between length of moonlight and activity overlap of petrels and gulls  $(\log_{10}O_{xy})$ .

rather than reacting directly to the present light intensity. On 13-14 May, a half-moon night (moonrise at 2300) with dense fog, the peak of petrel activity occurred at 0030 rather than 2200, as would be expected if there had been no fog (the data of this day were excluded in the numerical analysis). It seems, therefore, that petrel activity is not controlled only by endogenous rhythms keyed to lunar cycles, as reported in fruit bats (Morrison 1978). Because of the low visibility on 13-14 May, petrels might have found it more difficult to locate the island and thus delayed their arrival. This suggests that petrel activity at the colony was influenced by light intensity, anticipation of the lunar cycle, and weather conditions.

On nights with a full moon, petrel activity was highly synchronized in May, June, and August but was dispersed in September (Fig. 2). The synchrony of petrel activity at night was positively correlated to the length of moonlight time in May, June, July, and August (r = 0.843, n = 14,  $F_{1,12} = 29.47$ , P < 0.01) but not in September (Fig. 5).

Predation by gulls.—The number of flying gulls remained high in May, June, and August, but decreased in September ( $F_{4,13} = 5.45$ , P < 0.01; Table 2) because nonbreeders and unsuccessful breeders left the colony in August and September. The total number of petrels was large in May, June, and July, decreased in August, and was small in September ( $F_{4,13} = 8.59$ , P < 0.01;

#### YUTAKA WATANUKI



Fig. 5. The correlation between length of moonlight and synchrony of petrel activity shown by the  $I\delta$  index.  $\bullet = May$ ,  $\blacktriangle = June$ ,  $\blacktriangledown = July$ ,  $\blacksquare = August$ , and O = September. Regression line a is for the data of May, June, July, and August; b is for those of September.

Table 2). The number of petrels flying at night was positively correlated with the dry-weight percentage of petrel remains (Appendix 2) in the gull diets sampled in each 5-day period (r = 0.886, n = 18,  $F_{1,16} = 58.42$ , P < 0.01).

Monthly changes in petrel numbers, numbers killed by gulls, and predation rates are shown in Table 3. Gulls ate many petrels in May and June, more in July, fewer in August, and few in September, a pattern matching the seasonal cycle of estimated gull energy requirements (Appendix 1) and food composition (Appendix 2). Thus, the monthly petrel kill appears to vary with gull energy requirements and availability of the prey.

## DISCUSSION

Predator avoidance.—Slaty-backed Gulls are the most important predators of adult petrels on Daikoku Island. I estimated that annual predation by the gulls approximates 13.2% of all adult petrels. This appears to be a potentially strong selection pressure on Leach's Storm-Petrel, whose adult survival rate is high (Huntington and Burtt 1970).

The daily activity pattern of adult petrels

around the colony is crucial in avoiding gull predation. Petrel adults, eggs, and chicks in the nest burrows are protected from gull predation, and petrel foraging areas do not overlap those of gulls (Pearson 1968, Wiens and Scott 1975). Therefore, only adult petrels flying on or near colonies are subject to gull predation.

The negative correlation between petrel and gull activity levels (Fig. 3) indicates that predator avoidance may be the leading cause of petrel nocturnal behavior at Daikoku. Petrels avoided moonlight in May and June when the predation rate was relatively high, but they did not avoid it in September when the predation rate was minimal (Fig. 3, Table 3). The partial correspondence between seasonal change in predation rates and seasonal variation in moonlight effects on petrel activity further supports this hypothesis.

The medium synchrony of petrel activity on nights with half-moons (Fig. 5) probably was the result of short periods of darkness in which petrels were free from predation. The greatest activity synchrony occurred on nights with the highest predation risk (full-moon nights in May, June, and August) and the least synchrony on the night without predation risk (September; Fig. 5). Numbers of flying gulls were relatively constant on the full-moon nights compared with those of petrels (Fig. 2). Therefore, highly synchronous petrel activity on these nights may dilute the predator's effects by minimizing the risk that a particular petrel encounters a gull (Wilson 1975: 41-42).

Nest duties.—Although I could not distinguish nonbreeders from breeders during observations, nonbreeders were inferred to be abundant in June and July (Ainley et al. 1974), and probably in May, because the total number of flying petrels was high in these months (Table 2). Moonlight avoidance behavior disappeared in August and September; therefore, only nonbreeders may avoid moonlight. Because nonbreeders do not have as many nest duties as breeders, the threat of predation would be a crucial factor determining their activity pattern. Eight of 12 pairs exchanged their incubation duties on a clear, moonlit night (8-9 July). This implies that moonlight does not restrict breeders' activities during the incubation period, although more data are needed to substantiate this. Harris (1966) reported moonlight avoidance behavior in nonbreeding Manx

	May	June	July	Aug	Sept
No. of days observed	4	3	4	3	4
No. of petrels $(\bar{x})$	1,330.3	1,516.7	1,493.8	861.3	187.0
No. of gulls $(\bar{x})$	316.5	340.7	350.5	305.7	152.3

TABLE 2. Monthly change in the mean of the total number of flying birds in 24 h.

Shearwaters, which were killed by Herring Gulls (*L. argentatus*) and Great Black-backed Gulls (*L. marinus*) (Harris 1965).

On the other hand, seasonal changes in the nest duties of breeders may contribute to the seasonal changes in the petrel response to moonlight. Breeding petrels returned to the colony more frequently in the nestling period than in the incubation period. The relative importance of nest duties in the prelaying period may be small because prelaying exodus is suggested in Leach's Storm-Petrel (Gross 1935, Watanuki 1985b). I assumed, therefore, that nestduty activity was seasonal and correlated with the growth of chicks (Table 1). High predation risk and low nest duties seemed to cause breeders to avoid moonlight in May and June, but increasing nest duties in July might have taken priority over the high predation risk and consequently changed breeders' response to moonlight.

Bédard (1976) criticized the predator-avoidance hypothesis (Cody 1973) because there is intense predation on some alcid colonies in the Arctic, where daylight is continuous during the summer. On South Orkney Island ( $60^{\circ}43'S$ ,  $45^{\circ}38'W$ ), where the period of darkness is short in summer, the Black-bellied Storm-Petrel (*Fregetta tropica*) is preyed on by the diurnal Great Skua (*Catharacta skua*) and shows nocturnal activity (Beck and Brown 1971). Leach's Storm-Petrels on Kent Island ( $44^{\circ}02'N$ ,  $124^{\circ}09'W$ ) and on Little River Rock ( $41^{\circ}02'N$ ,  $124^{\circ}09'W$ ) also are killed by diurnal gulls and show nocturnal activity (Gross 1935) as well as moonlight avoidance behavior (Harris 1974). On the other hand, Audubon's Shearwaters (*Puffinus lherminieri*) and Galapagos Storm-Petrels (*Oceanodroma tethys*) are diurnal on their breeding island, where the most important predator is a nocturnal or crepuscular owl (*Asio galapagoensis*; Harris 1969a, b). Thus, although the predatoravoidance hypothesis generally is supported, further investigations on intercolonial and interspecific variation of predation risk and diurnal activity patterns are needed.

Foraging.-Grubb (1974) suggested that abundant food in the ocean's upper waters at night has been a strong selective force toward nocturnal activity of Leach's Storm-Petrels at sea. Food of Leach's Storm-Petrels breeding on Daikoku Island may be most abundant at night (Watanuki 1985a). The petrels stay on the island for part of the night and thus lose some opportunities for feeding at night when prey is abundant. A pair exchanges incubation duties at night every 2.9 days, and hence it loses one night of feeding opportunities about every 3 days. Missed feeding opportunities seem to be potentially crucial because a petrel must recover 11% of body weight lost during an incubation stint (Watanuki 1985b). In addition, a pair feeds a chick at least 1.2 times per night and thus loses more opportunities.

Sensory constraints probably affect foraging time. If Leach's Storm-Petrels rely heavily on visual cues to locate food, they would have the advantage of feeding during the day or on a moonlit night. Leach's Storm-Petrels can locate food by smell at night as well as during the

TABLE 3. Monthly change in the number of petrels potentially available, number killed by gulls, and predation rate.

	May	June	July	Aug	Sept
No. of petrels <sup>a</sup>	987,700	908,700	760,500	589,300	547,800
No. killed	36,676	29,376	49,065	15,176	321
Predation rate (%)	3.7	3.2	6.5	2.6	0.1

\* Includes nonbreeders in May, June, and July. Nonbreeders were assumed to be 16% of the total population (Wiens and Scott 1975). Unsuccessful breeders were assumed to have left the colony as soon as they failed.

day (Grubb 1972). Gordon (1955) suggested that they are nocturnal feeders, although they also feed during the day (H. Ogi pers. comm.). Direct tests of Grubb's hypothesis are lacking. Indirect evidence suggests that the petrels are not obligatory nocturnal feeders and that abundant prey at night is not always an important factor affecting the petrels' nocturnal activity at the breeding colony. In conclusion, predation risk and nest duties seem to be more important factors determining petrel activity at the colony than food availability.

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## LITERATURE CITED

- ABE, M., N. ICHIDA, H. SHIMIZU, M. HASHIMOTO, O. YUNOKI, N. OZAWA, & S. OZAWA. 1972. [A new attempt to estimate the number of nesting petrel, Oceanodroma leucorhoa leucorhoa, and wildlife of the Daikoku Island, Hokkaido.] Tori 21: 346-365.
- AINLEY, D. G., S. MORRELL, & T. J. LEWIS. 1974. Pattern in the life histories of storm petrels on the Farallon Islands. Living Bird 13: 295-312.
- BECK, J. R., & D. W. BROWN. 1971. The breeding biology of the Black-bellied Storm-Petrel Fregetta tropica. Ibis 113: 73-90.
- BÉDARD, J. 1976. Coexistence, coevolution and convergent evolution in seabird communities: a comment. Ecology 57: 177–184.
- BOERSMA, P. D., N. T. WHEELWRIGHT, M. K. NERINI, & E. S. WHEELWRIGHT. 1980. The breeding biology of the Fork-tailed Storm-Petrel (Oceanodroma furcata). Auk 97: 268-282.
- BRISBIN, I. L., JR. 1968. A determination of the caloric density and major body components of large birds. Ecology 49: 792–794.
- CODY, M. L. 1973. Coexistence, coevolution and convergent evolution in seabird communities. Ecology 54: 31-44.
- FURNESS, R. W. 1978. Energy requirements of seabird communities: a bioenergetic model. J. Anim. Ecol. 47: 39–53.
- GORDON, M. S. 1955. Summer ecology of oceanic birds off southern New England. Auk 72: 138– 147.
- GROSS, W. A. O. 1935. The life history cycle of Leach's Petrel (Oceanodroma leucorhoa leucorhoa) on outer sea islands of the Bay of Fundy. Auk 52: 328–399.

- GRUBB, T. C. 1972. Smell and foraging in shearwaters and petrels. Nature 237: 404-405.
- . 1974. Olfactory navigation to the nesting burrow in Leach's Petrel (Oceanodroma leucorhoa). Anim. Behav. 22: 192-202.
- HARRIS, M. P. 1965. The food of some Larus gulls. Ibis 107: 43-53.
- ——. 1966. Breeding biology of Manx Shearwater Puffinus puffinus. Ibis 108: 17-33.
- ——. 1969a. Food as a factor controlling the breeding of Puffinus lherminieri. Ibis 111: 432-456.
- ———. 1969b. The biology of storm petrels in the Galápagos Islands. Proc. California Acad. Sci. 37: 95–166.
- HARRIS, S. W. 1974. Status, chronology and ecology of nesting storm-petrels in northern California. Condor 76: 249-261.
- HUNT, G. L., JR. 1972. Influence of food distribution and human disturbance on the reproductive success of Herring Gulls. Ecology 53: 1051–1061.
- HUNTINGTON, C. E., & E. H. BURTT, JR. 1970. Breeding age and longevity in Leach's Petrel Oceanodroma leucorhoa. Abstr., 15th Intern. Ornithol. Congr.: 663.
- MANUWAL, D. A. 1974. The natural history of Cassin's Auklet (*Ptychoramphus aleuticus.*). Condor 76: 421-431.
- MORISHITA, M. 1959. Measuring of dispersion of individual and analysis of distribution patterns. Mem. Fac. Sci., Kyushu Univ. Ser. E, Biol. 2: 215-235.
- MORRISON, D. W. 1978. Lunar phobia in a neotropical fruit bat Artibeus jamaicensis (Chiroptera: Phyllostomidae). Anim. Behav. 26: 852–855.
- PEARSON, T. H. 1968. The feeding biology of seabird species breeding on the Farne Islands, Northumberland. J. Anim. Ecol. 37: 521-552.
- PIANKA, E. R. 1973. The structure of lizard communities. Ann. Rev. Ecol. Syst. 4: 53-74.
- SIBLY, R. M., & R. H. MCCLEERY. 1983. Increase in weight of Herring Gulls while feeding. J. Anim. Ecol. 52: 35–50.
- SOKAL, R. R., & F. J. ROHLF. 1969. Biometry. San Francisco, W. H. Freeman and Co.
- THORESEN, A. C. 1964. The breeding behavior of the Cassin Auklet. Condor 66: 456-476.
- WATANUKI, Y. 1984. Food intake and pellet of Blacktailed Gull, Larus crassirostris. J. Yamashina Inst. Ornithol. 16: 168–169.
- ——. 1985a. Food of breeding Leach's Storm-Petrels (Oceanodroma leucorhoa). Auk 102: 884–886.
- ———. 1985b. Breeding biology of Leach's Storm-Petrels Oceanodroma leucorhoa on Daikoku Island, Hokkaido, Japan. J. Yamashina Inst. Ornithol. 17: 9–22.
- WIENS, J. A., & J. M. SCOTT. 1975. Model estimation of energy flow in Oregon coastal seabird populations. Condor 77: 439-452.

- WILBUR, H. M. 1969. The breeding biology of Leach's Storm-Petrel Oceanodroma leucorhoa. Auk 86: 433-442.
- WILSON, E. O. 1975. Sociobiology, a new synthesis. Cambridge, Massachussetts, Belknap Press.

#### **APPENDIX** 1

Calculation of energy requirements of the Slaty-backed Gull.-A model similar to Furness's (1978) was used to estimate the energy requirement of Slaty-backed Gulls. Egg-laying, hatching, chick survival, and chick growth were monitored at 5-day intervals in the 4 study quadrats (Fig. 6). Mean daily energy requirements for egg production, chick existence, and chick growth at 5-day intervals were then estimated. The average percentage of time spent foraging away from the nest site by adults was determined by monitoring 10-20 pairs at nest sites every 30 min at night using a starlight scope. Birds away from the nests were assumed to be foraging in flight. Seasonal changes in the foraging time of breeders are shown in Fig. 6b. Percentage of flapping flight, measured by scanning flying birds for 1 min every 5 min in various wind conditions, averaged 50%. Breeders' activity requirements were estimated from foraging time, percentage of flapping flight, and energy costs of flapping and gliding flight. Foraging times of nonbreeders were not measured, but were assumed to be similar to that of breeders. Existence energy requirements of adults and chicks were estimated from their body weight and the mean daily ambient temperature.

I counted the number of adults on breeding sites and surrounding areas about every 3 weeks. About 5,000 birds were on the breeding sites in June and July. Nest-site tenacity of parents during daytime in these months was about 70%; accordingly, the number of breeders was estimated to be about 7,000. About 2,000 birds were in surrounding areas and were assumed to be nonbreeders at their maximum number in late May.

Other species-specific parameters are: egg weight at laying, 107 g (n = 25); adult weight, 1,100 g (n =1); arrival of last breeder, 1 May; departure of first breeder, 30 July; departure of last breeder, 25 September; date of peak number of nonbreeders, 26 May. The following dates were assumed: arrival of first breeder, 1 March; arrival of first nonbreeder, 1 April; departure of last nonbreeder, 30 July. Model-specific parameters are the same as in Furness (1978).

## APPENDIX 2

Laying 100 No, /5 days Hatching 50 Fledging b 12 10 h/day 8 6 4 2 c kcal.x 10<sup>6</sup> ⁄ 5 days Total 20 15 Breeder 10 Chick 5 Nonbreeder Sep. Jun. Jul Apr Mav Aug

Fig. 6. Breeding phenology and energy requirements of Slaty-backed Gulls. (a) Seasonal changes in egg-laying, hatching, and fledging; (b) number of hours of foraging activity per day; (c) energy requirements. The curves in (c) represent the increasing energy requirements of nonbreeders, chicks, breeders, and the total population.

Food of Slaty-backed Gulls.—Pellets and food remains were dried to constant weight at about 20°C

Fig. 7. Seasonal changes in diet of Slaty-backed Gulls shown by dry-weight percentages. (a) Adult Leach's Storm-Petrel; (b) fish (dark line) and other items (broken line).



for at least 30 days. Adult Leach's Storm-Petrels, fish, shellfish, crabs, and chickens were the main food items. The following equation was used to determine the total wet weight of the *i*th food:  $W_i = (D_i \times R_i \times TER)/(\Sigma D_i R_i C_i)$ , where  $D_i = dry$  weight of the *i*th food,  $R_i =$  regurgitation coefficient of the *i*th food (showing the ratio between wet weight of intake and dry weight of pellets), TER = total energy requirement of the gulls for 5 days, and  $C_i =$  caloric value of the *i*th food.  $C_i$ s (kcal/kg wet weight) were assumed to be the following: adult Leach's Storm-Petrel, 2,600;

fish, 1,500; crab with shell, 700; shellfish with shell, 500; chicken, 3,000 (Brisbin 1968, Hunt 1972, Sibly and McCleery 1983). R<sub>5</sub> were assumed to be the same as those of Black-tailed Gulls (*Larus crassirostris*) and the following: adult Leach's Storm-Petrel, 5.9; fish, 317.3; crab, 6.7; shellfish, 2.2; chicken, 30.0 (Watanuki 1984). The number of petrels killed by gulls was calculated by dividing the total petrel wet weight by the average individual adult weight (48 g, Watanuki 1985b). Seasonal changes in the gulls' diet composition are shown in Fig. 7.

### (continued from p. 13)

in male Black-headed Grosbeaks; Adan (Hussein) Isack, biology of the Greater Honeyguide (Indicator indicator); Dr. Pedro Jordano, pattern of fruit use by wintering frugivorous birds and their implications for birddispersed plants in Mediterranean habitats; Frank J. Joyce, nest site selection by three passerine associates of Hymenoptera; Donald M. Kent, foraging strategies of Snowy Egrets (Egretta thula) in the salt marshes of Massachusetts; Roni King, winter territoriality in migratory European Robins (Erithacus rubecula)-habitat selection and winter survivorship; Francis R. Lambert, co-adaptation between frugivorous birds and fig trees in Malaysian lowland forest; Jeanette L. Lebell, microgeographic variation in the flight whistle of the Brownheaded Cowbird; David E. Manry, a preliminary study of blood and feather pulp proteins in two South American ibis (Threskiornithidae) species; Jean-Louis Martin, the population structure of Parus caeruleus L. (Aves): geographical variation and speciation in the Mediterranean region; Jon Miller, breeding distribution and origin of Water Pipits in the Sierra Nevada; David Morimoto, effects of forest fragmentation on avian community structure and species-habitat relationships in the southeastern Massachusetts Pine Barrens; Jay Pitocchelli, speciation in the genus Oporornis; Richard O. Prum, courtship behavior and ecology of Masius chrysopterus in Ecuador; Dr. Michael R. W. Rands, the breeding behavior and habitat of the Arabian Bustard, Ardeotis arabs; Pamela C. Rasmussen, relationships of Fuego-Patagonian Blue-eyed Shags; Mark D. Reynolds, social behavior of Yellow-billed Magpies; Dr. Gary Ritchison, the significance of song repertoires in the Northern Cardinal; Jeffrey A. Schwartz, vocal similarity in mated Ring-billed Gulls as an aid in parental recognition by young; Dr. Ron Scogin, floral color and hummingbird vision; Peter E. Scott, the nesting ecology of desert hummingbirds in relation to the pollination ecology of certain nectar plants; Patricia Serrentino, the breeding ecology and behavior of the Northern Harrier (Circus cyaneus) in Coos County, New Hampshire; Laurie J. Stuart-Simons, food limitation in birds; Richard R. Snell, hybridization, isolation and species recognition in arctic gulls; Carol Spaw, thick-shelled eggs and their evolutionary implications; Charles Sullivan, nest behavior and development of young in the Jabiru Stork; Dr. Kimberly A. Sullivan, energetics and the development of time-budgeting; Richard John Watling, investigation of status of Ogea Flycatcher and Blue-crowned Lory; Dr. G. Causey Whittow, water loss from eggs of Great Frigatebird (Fregata minor); Dr. David Winkler, a general model of parental care with experimental tests on the Tree Swallow; John L. Zimmerman, Ortstreue in Henslow's Sparrows (Ammodramus henslowii) and movements in response to spring burning of tallgrass prairie.