HEDRICK, P. W. 1983. Genetics of populations. Boston, Science Books Int.

HOPKINSON, D. A., & H. HARRIS. 1969. Red cell acid phosphatase, phosphoglucomutase, and adenylate kinase. Pp. 337-375 *in* Biochemical methods in red cell genetics (J. J. Yunis, Ed.). New York, Academic Press.

INTERNATIONAL UNION OF BIOCHEMISTRY. 1984. Enzyme nomenclature. New York, Academic Press.

JOHNSGARD, P. A. 1973. Grouse and quails of North America. Lincoln, Univ. Nebraska Press.

LEWIS, J. B. 1954. Further studies of bob-white mobility in central Missouri. J. Wildl. Manage. 18: 414-416.

MANLOVE, M. N., J. C. AVISE, H. O. HILLESTAD, P. R. RAMSEY, M. H. SMITH, & D. O. STRANEY. 1975. Starch gel electrophoresis for the study of population genetics in white-tailed deer. Proc. Annu. Conf. Southeastern Assoc. Game & Fish Comm. 29: 392-403.

MATSON, R. H. 1984. Applications of electrophoretic data in avian systematics. Auk 101: 717-729.

MCALPINE, P. J., N. VAN CONG, C. BOUCHEIX, A. J. PAKSTIS, R. C. DOUTE, & T. B. SHOWS. 1987. The 1987 catalog of mapped genes and report of the nomenclature committee. Cytogenet. Cell Genet. 46: 29-101.

MURPHY, D. A., & T. S. BASKETT. 1952. Bobwhite mobility in central Missouri. J. Wildl. Manage. 16: 498-510.

NEI, M., & R. K. CHESSER. 1983. Estimation of fixation indices and gene diversities. Ann. Hum. Genet. 47: 253-259.

POULIK, M. D. 1957. Starch gel electrophoresis in a discontinuous system of buffers. Nature 180: 1477-1479.

ROCKWELL, R. F., & G. F. BARROWCLOUGH. 1987. Gene flow and the genetic structure of populations. Pp. 223-255 *in* Avian genetics (F. Cooke and P. A. Buckley, Eds.). New York, Academic Press.

ROGERS, J. S. 1972. Measures of genetic similarity and genetic distance. Studies in genetics—VII. Univ. Texas Publ. 7213: 145-153.

ROSEBERRY, J. L., & W. D. KLIMSTRA. 1984. Population ecology of the bobwhite. Carbondale, Illinois, Southern Illinois Univ. Press.

ROSENE, W. 1969. The Bobwhite Quail: its life and management. New Brunswick, New Jersey, Rutgers Univ. Press.

SELANDER, R. K., M. H. SMITH, S. Y. YANG, W. E. JOHNSON, & J. B. GENTRY. 1971. Biochemical polymorphism and systematics in the genus *Peromyscus*—I. Variation in the old-field mouse (*Peromyscus polionotus*). Studies in genetics—VI. Univ. Texas Publ. 7103: 49-90.

SLATKIN, M. 1977. Gene flow and genetic drift in a species subject to frequent local extinctions. Theor. Popul. Biol. 12: 253-262.

———. 1985a. Gene flow in natural populations. Annu. Rev. Ecol. Syst. 16: 393-430.

———. 1985b. Rare alleles as indicators of gene flow. Evolution 39: 53-65.

———. 1987. Gene flow and the geographic structure of natural populations. Science 236: 787-792.

STODDARD, H. L. 1931. The Bobwhite Quail: its habits, preservation, and increase. New York, Charles Scribner's Sons.

VAN DEN BUSSCHE, R. A., M. J. HAMILTON, & R. K. CHESSER. 1986. Problems of estimating gene diversity among populations. Texas J. Sci. 38: 281-287.

ZINK, R. M., D. F. LOTT, & D. W. ANDERSON. 1987. Genetic variation, population structure, and evolution of California Quail. Condor 89: 395-405.

Received 7 November 1988, accepted 21 February 1989.

Gull Predation on Cassin's Auklet Varies with the Lunar Cycle

DOUGLAS A. NELSON[1]

Museum of Zoology, University of Michigan, Ann Arbor, Michigan 48109 USA, and
Point Reyes Bird Observatory, 4990 Shoreline Highway, Stinson Beach, California 94970 USA

Many species of small burrow-nesting seabirds visit their breeding colonies only at night. Nocturnal activity has usually been thought to be a defense against predation (Lack 1966, Cody 1973, Ainley et al. 1975), although diel-cycle variation in the availability of food may also play a role in determining the timing of colony visits (Grubb 1974, Imber 1975). Activity in seabird colonies is reduced on moonlit nights (Cassin's Auklet, *Ptychoramphus aleuticus*, Manuwal 1974a, Ainley and Boekelheide 1989; Manx Shearwater, *Puffinus puffinus*, Harris 1966, Storey and Grimmer 1986; Leach's Storm-Petrel, *Oceanodroma leucorhoa*, Watanuki 1986; Ashy Storm-Petrel, *O. homochroa*, Ainley and Boekelheide 1989; Madeiran Storm-Petrel, *O. castro*, Harris 1969), but it has not been shown that predation risk is a correlate of the lunar cycle. I found that Cassin's Auklets on Southeast Farallon Island

[1] Present address: Rockefeller University, Field Research Center, Box 38B, RR 2, Tyrrel Road, Millbrook, New York 12545 USA.

(SEFI), California, suffer heavier predation by Western Gulls (*Larus occidentalis*) on moonlit nights than on dark nights.

Cassin's Auklet is a small (180 g) burrow-nesting alcid that is strictly nocturnal at the SEFI colony. It is the most abundant species breeding on SEFI (ca. 100,000 adults; Manuwal 1974a, Ainley and Boekelheide 1989). Auklets excavate burrows in the soil along a level marine terrace on the island's south side (see map *in* Ainley and Lewis 1974: 439) and nest in rock crevices wherever they are available. The majority of the island's 22,000–25,000 Western Gulls also nest on the marine terrace.

Auklet arrival and departure from the colony vary with ambient light conditions and stage of the breeding cycle (Manuwal 1974a, Ainley and Boekelheide 1989, pers. obs.). On dark nights throughout the breeding season and on moonlit nights during the incubation and chick-rearing periods, auklets begin arriving within 30 min after dark. From 1970 to 1983, Ainley and Boekelheide (1989) found that bright nights suppress the frequency of colony visits by ca. 20% before egg laying and decrease above-ground activity throughout the breeding cycle. On bright nights, auklets arrive later and depart earlier, and spend ca. 30% less time on land than on dark nights (Ainley and Boekelheide 1989). Most auklets depart the island 1–2 h before sunrise.

To estimate predation on auklets, I walked a 300-m-long concrete path before sunrise on 81 days between 29 February and 15 July 1980. The path followed the railway shown on the map in Ainley and Lewis (1974: 439), beginning at the western quarters and extending to the eastern end of the island. I timed my walk each morning to coincide with the first light sufficient for me to see (0430–0545 PST). This reduced the chance that gulls would remove auklets from the study area (or consume them) before they were counted. I counted every dead auklet visible within 15 m of either side of the path. Thirty-two carcasses were salvaged, aged (Manuwal 1978), and sexed by dissection. I also recorded weather conditions (clear to partly cloudy, cloudy, or foggy) and stage of the moon each morning.

Approximately 1,635 auklet pairs and 51 Western Gull pairs nested within the 9,000-m^2 sample area. The sampling dates included all stages of the breeding cycle. Egg laying began on 17 April 1980 ($\bar{x}$ = 28 April) in a plot of 29 nests located 30 m west of the sample area. Incubation of the single egg lasts an average of 38 days, followed by a nestling period of 41 days (Manuwal 1974a). I divided the breeding cycle into three stages: pre-egg (before 28 April), incubation (29 April to 5 June), and nestling (after 5 June).

I plotted the frequency of dead auklets as a function of days after full moon, and used circular statistical methods (Zar 1974) to calculate the mean and standard deviation of auklet numbers found over the lunar cycle. I used a *G*-test to fit the observed frequency distribution to one expected by random sampling over a lunar cycle divided into four 7- or 8-day periods, centered on full moon, last quarter, new moon, and first quarter. Expected frequencies within each period equaled the total number of auklets found multiplied by the percentage of the total number of sampling days within the period.

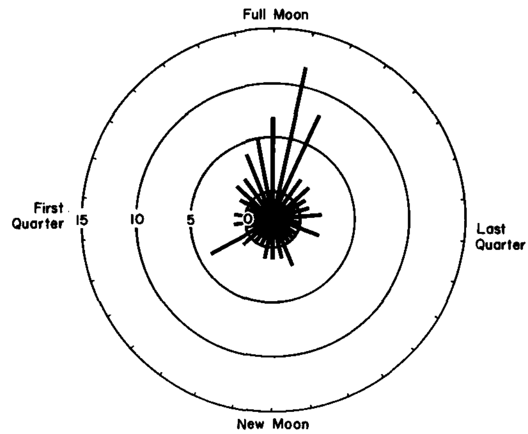

Fig. 1. Frequency distribution of auklets (n = 63) found dead at dawn on 81 days as a function of the lunar cycle.

I counted 63 dead auklets on the 81 days: 56 adults, 4 subadults, and 3 fledglings. Most were being eaten by Western Gulls at the time of discovery. With full moon defined as 0°, the mean of the frequency distribution (Fig. 1) was 4.3° (standard deviation = 63.56°). Because 12° corresponds to 1 day over a 30-day lunar cycle, most auklets were killed within 5 days of full moon. The frequency distribution was significantly non-uniform over the 4 lunar phases ($G = 38.7$, df = 3, $P < 0.005$). Clouds or fog during the full moon phase did not decrease the number of auklets killed compared with clear or partly cloudy moonlit nights (cloudy: $\bar{x} = 4.20 \pm 3.35$, $n = 14$; clear: $\bar{x} = 3.50 \pm 2.82$, $n = 14$; Mann-Whitney $U = 95$, $P > 0.90$).

The number of auklets found per day increased as the breeding season progressed (Spearman's rho = 0.20, $n = 81$, $P < 0.05$). This probably reflects greater rates of colony visitation by breeders during the incubation and nestling stages (auklet pairs exchange incubation duties and feed their single chick nightly), and also increased attendance by nonbreeders. Four male subadult auklets were found at dawn between 29 May and 11 July, which implies that young nonbreeders do not visit land until late in the breeding season (Nelson 1981). The correlation between mortality and date did not bias the association between mortality and lunar phase because sampling was distributed uniformly with respect to lunar phase and the breeding cycle ($G = 7.0$, df = 4, $P > 0.10$). The last and first quarters were lumped into one category (half moon) to avoid small expected values.

Manuwal (1979) found that fledglings outnumbered adults in a collection of dead auklets in July 1971. Had my study been continued, fledglings may have become more common. The 3 fledglings were found on 29 June, 2 July, and 7 July, early in the fledging period that began on 3 July.

Western Gulls probably killed most, if not all, of the auklets. Thoresen (1964) and Manuwal (1979) also described heavy predation by gulls on SEFI. The last Peregrine Falcon (*Falco peregrinus*) in 1980 was observed on the island on 15 April (Point Reyes Bird Observatory [PRBO] unpubl. data). Peregrines were not near any of the 9 auklet carcasses found before 15 April. I conclude that moonlight enabled gulls to capture auklets prior to the pre-dawn exodus.

Leach's and Ashy storm-petrels, two other nocturnal seabirds on SEFI, also suffer predation by gulls (Ainley et al. 1975). These species, with a combined Farallon population of ca. 5,400 breeding birds (Ainley and Lewis 1974), appear to reduce the risk of gull predation by nesting in areas of the island with few gulls. Storm-petrels respond to moonlight as do auklets (Ainley and Boekelheide 1989). The expansion of the gull population into storm-petrel breeding areas (PRBO unpubl. data) may portend increased predation on these species. In auklets, competition for nesting space is so intense on SEFI (Manuwal 1974b), and gulls are so abundant, that most auklets do not have the option of choosing nest sites away from gulls. Instead, decreased colony activity on moonlit nights appears to minimize the risk of predation by gulls.

I thank the Point Reyes Bird Observatory and the Farallon Patrol of the Oceanic Society (San Francisco Bay Chapter) for logistic support. The San Francisco Bay National Wildlife Refuge granted permission to work on the Farallones. David Ainley made helpful comments on the manuscript. This is Contribution No. 414 of the Point Reyes Bird Observatory.

Literature Cited

AINLEY, D. G., & R. J. BOEKELHEIDE (Eds.) 1989. Seabirds of the Farallon Islands: ecology, structure, and dynamics of an upwelling-system community. Palo Alto, California, Stanford Univ. Press.

———, & T. J. LEWIS. 1974. The history of the Farallon Island marine bird populations, 1854–1972. Condor 76: 432–446.

———, S. MORRELL, & T. J. LEWIS. 1975. Patterns in the life histories of storm petrels on the Farallon Islands. Living Bird 13: 295–312.

CODY, M. L. 1973. Coexistence, coevolution and convergent evolution in seabird communities. Ecology 54: 31–44.

GRUBB, T. C., JR. 1974. Olfactory navigation to the nesting burrow in Leach's Petrel (*Oceanodroma leucorhoa*). Anim. Behav. 22: 192–202.

HARRIS, M. P. 1966. Breeding biology of Manx Shearwater *Puffinus puffinus*. Ibis 108: 17–33.

———. 1969. The biology of storm petrels in the Galapagos Islands. Proc. Calif. Acad. Sci. 37: 95–166.

IMBER, M. J. 1975. Behaviour of petrels in relation to the moon and artificial lights. Notornis 22: 302–306.

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

MANUWAL, D. A. 1974a. The natural history of Cassin's Auklet (*Ptychoramphus aleuticus*). Condor 76: 421–431.

———. 1974b. Effects of territoriality on breeding in a population of Cassin's Auklet. Ecology 55: 1399–1406.

———. 1978. Criteria for aging Cassin's Auklets. Bird-Banding 49: 157–161.

———. 1979. Reproductive commitment and success of Cassin's Auklet. Condor 81: 111–121.

NELSON, D. A. 1981. Sexual differences in measurements of Cassin's Auklet. J. Field Ornithol. 52: 233–234.

STOREY, A. E., & B. L. GRIMMER. 1986. Effect of illumination on the nocturnal activities of Manx Shearwaters: colony avoidance or inconspicuous behaviour? Bird Behav. 6: 85–89.

THORESEN, A. 1964. Breeding behavior of the Cassin Auklet. Condor 66: 456–476.

WATANUKI, Y. 1986. Moonlight avoidance behavior in Leach's Storm-Petrels as a defense against Slaty-backed Gulls. Auk 103: 14–22.

ZAR, J. H. 1974. Biostatistical Analysis. Englewood Cliffs, New Jersey, Prentice-Hall, Inc.

Received 21 December 1988, accepted 16 March 1989.