

- CLAYTON, N. S. 1987. Song tutor choice in Zebra Finches. *Anim. Behav.* 35:714-721.
- HIEBERT, S. M., P. K. TODDARD, AND P. ARCESE. 1989. Repertoire size, territory acquisition and reproductive success in the Song Sparrow. *Anim. Behav.* 37:266-273.
- HULTSCH, H., AND D. TODT. 1989a. Memorization and reproduction of songs in nightingales (*Luscinia megarhynchos*): evidence for package formation. *J. Comp. Physiol. A.* 165:197-203.
- HULTSCH, H., AND D. TODT. 1989b. Song acquisition and acquisition constraints in the nightingale, *Luscinia megarhynchos*. *Naturwissenschaften* 76:83-85.
- KROODSMA, D. E. 1977. A re-evaluation of song development in the Song Sparrow. *Anim. Behav.* 25:390-399.
- KROODSMA, D. E., AND R. PICKERT. 1984. Repertoire size, auditory templates, and selective vocal learning in songbirds. *Anim. Behav.* 32:395-399.
- MARLER, P. 1991. Song-learning behavior: the interface with neuroethology. *Trends Neurosci.* 14:199-206.
- MARLER, P., AND S. PETERS. 1982. Long-term storage of learned birdsongs prior to production. *Anim. Behav.* 30:479-482.
- MARLER, P., AND S. PETERS. 1987. A sensitive period for song acquisition in the Song Sparrow, *Melospiza melodia*: a case of age-limited learning. *Ethology* 76:89-100.
- MARLER, P., AND S. PETERS. 1988. The role of song phonology and syntax in vocal learning preferences in the Song Sparrow, *Melospiza melodia*. *Ethology* 77:125-149.
- NOWICKI, S., P. MARLER, A. MAYNARD, AND S. PETERS. 1992. Is the tonal quality of birdsong learned? Evidence from Song Sparrows. *Ethology* 90:225-235.
- OKANOYA, K., AND R. J. DOOLING. 1988. Hearing in the Swamp Sparrow, *Melospiza georgiana*, and the Song Sparrow, *Melospiza melodia*. *Anim. Behav.* 36:726-732.
- PEPPERBERG, I. 1988. The importance of social interaction and observation in the acquisition of communicative competence: possible parallels between avian and human learning, p. 279-299. *In* T. R. Zentall and B. G. Galef, Jr. [eds.], *Social learning: psychological and biological perspectives*. Lawrence Erlbaum, Hillsdale, NJ.
- PETERS, S., W. A. SEARCY, AND P. MARLER. 1980. Species song discrimination in choice experiments with territorial male Swamp and Song Sparrows. *Anim. Behav.* 28:393-404.
- PETRINOVITCH, L. 1985. Factors influencing song development in the White-crowned Sparrow (*Zonotrichia leucophrys*). *J. Comp. Psychol.* 99:15-29.
- SEARCY, W. A., AND P. MARLER. 1981. A test for responsiveness to song structure and programming in female sparrows. *Science* 213:926-928.
- SEARCY, W. A., P. D. McARTHUR, S. PETERS, AND P. MARLER. 1981. Response of male Song and Swamp Sparrows to neighbor, stranger and self songs. *Behaviour* 77:152-163.
- SEARCY, W. A., P. D. McARTHUR, AND K. YASUKAWA. 1985. Song repertoire size and male quality in Song Sparrows. *Condor* 87:222-228.
- SLATER, P. J. B. 1983. Bird song learning: theme and variations, p. 475-499. *In* A. H. Brush and G. A. Clark, Jr. [eds.], *Perspectives in ornithology*. Cambridge Univ. Press, Cambridge, England.
- THIELCKE-POLTZ, H., AND G. THIELCKE. 1960. Akustisches lernen verschieden alter schallisolierter amslen (*Turdus merula* L.) und die entwicklung erlernter motive ohne und mit künstlichem einfluss von testosterone. *Z. Tierpsychol.* 17:211-244.
- TODT, D., H. HULTSCH, AND D. HEIKE. 1979. Conditions affecting song acquisition in nightingales (*Luscinia megarhynchos* L.). *Z. Tierpsychol.* 51:23-35.

The Condor 94:1019-1021
© The Cooper Ornithological Society 1992

ANNUAL SURVIVAL OF BREEDING CASSIN'S AUKLETS IN THE QUEEN CHARLOTTE ISLANDS, BRITISH COLUMBIA¹

ANTHONY J. GASTON

Canadian Wildlife Service, 100 Gamelin Blvd., Hull, Quebec K1A 0H3, Canada

Key words: Cassin's Auklet; *Ptychoramphus aleuticus*; survival rate.

Adult annual survival rate, which determines future life expectancy, is a basic demographic parameter fundamental to understanding population processes and life history strategies. Few estimates of adult survival

are available for auks. Among populations breeding on the Pacific Ocean coasts, estimates are available only for the Cassin's Auklet *Ptychoramphus aleuticus* (Speich and Manuwal 1974) and Pigeon Guillemot *Cepphus columba* (Nelson 1991), both on the Farallon Islands, California and for the Ancient Murrelet *Synthliboramphus antiquus* on the Queen Charlotte Islands, British Columbia (Gaston 1990).

I report here the results of seven years of trapping breeding Cassin's Auklets at a colony in the Queen

¹ Received 18 February 1992. Accepted 20 May 1992.

TABLE 1. Numbers of Cassin's Auklets captured and retrapped at Reef Island, British Columbia.

Year	Number trapped	Number banded that year	Year of recovery					
			1986	1987	1988	1989	1990	1991
1985	36	36	13	15	10	12	3	8
1986	31	18		5	1	1	0	0
1987	51	31			6	5	2	5
1988	44	27				0	0	1
1989	28	10					0	4
1990	6	1						1
1991	26	7						
Totals	222	130	13	20	17	18	5	19

Charlotte Islands. This area is 15° north of the Farallon Islands, and in a different oceanographic regime; one that is largely unaffected by episodic upwelling events which cause large year-to-year variation in breeding success of seabirds at the Farallon Islands (Ainley and Boekelheide 1990). I also compare the survival rate of breeding Cassin's Auklets with that of Ancient Murrelets breeding on the same island.

METHODS

The study took place on Reef Island (52°52'N, 131°31'W), in the Queen Charlotte Islands archipelago (for further details see Gaston 1990). This 300-ha island supports approximately 1,700 breeding pairs of Cassin's Auklets in a number of dense pockets around its periphery (Rodway et al. 1988). Birds were mist-netted close to their burrow entrances in the largest of these pockets of burrows on the southeast coast of the island, a locality known as "Cassin's Castle." Breeding burrows in this area are situated on a small bluff, in dense turf at the edge of a small cliff, about 60 m from the sea. Trapping was conducted on two to five nights annually during the late incubation and chick-rearing periods (May and the first half of June) in 1985–1991. The proportion of birds regurgitating food, and hence arriving to feed chicks, was similar in all years. This suggests that there was little year-to-year variation in timing of breeding. The mist net was always set in the same spot, and left erected from sunset (20:30–21:30 hr PDT) to about 03:00 hr. On all nights, more than

90% of captures were made within the first hour of arrivals. There was no indication that either tides or moonlight affected the attendance of birds feeding nestlings; these made up the majority of birds trapped in all years.

It would have been possible to restrict the survival rate analysis to birds that regurgitated food and hence to known breeders. However, this would have required omitting a number of recaptures (presumably birds still incubating, or failed breeders) and significantly reducing an already small sample size. General observations of behavior suggested that most non-breeders arrived well after midnight, landing at the cliff edge and hence avoiding capture in the mist net.

Adult annual survival rates were estimated by two methods; the SURGE capture-recapture program of Lebreton and Clobert (1986, version 4.0) and the regression method of Furness (1978). The treatment followed was that of Gaston (1990) in estimating the annual survival of Ancient Murrelets on the same island, to give maximum comparability between the estimates made for these two species. Like Ancient Murrelets, Cassin's Auklets showed much lower survival in the first year after banding than subsequently, presumably because trapping affected the chance of recapture in the following year. Consequently, for the SURGE estimate, I estimated survival in the first and subsequent years of recapture separately, and assumed that the latter estimate was representative of normal survival. I used Seber's (1973, as given in Gaillard et al. 1989) formula to estimate future life expectancy (Y) from estimates of annual survival rates (s):

$$Y = 0.5 + (1/[1 - s])$$

TABLE 2. Results of SURGE analysis of capture-recapture data for Cassin's Auklets at Reef Island.

Year	Estimate	95% Confidence Interval
Survival probabilities		
First	0.495	0.369–0.622
Subsequent	0.881	0.726–0.954
Recapture probabilities		
1986	0.499	0.313–0.686
1987	0.657	0.456–0.814
1988	0.447	0.275–0.632
1989	0.417	0.241–0.616
1990	0.113	0.044–0.261
1991	0.471	0.240–0.716

The SURGE program estimates the probability of recapture separately by years and hence is independent of year-to-year variations in effort (Clobert et al. 1987). Only years in which estimated recapture probabilities did not differ significantly from one another were included in the regression analysis, which was based on the recapture of birds banded only in 1985 and 1986. The recapture rates of birds banded in subsequent years were very low, presumably because by then most of the birds in the sampling area were banded. Consequently, those trapped for the first time in later years were likely to have been mainly prospectors. As the survival estimates calculated by SURGE are independent of sampling intensity, I included data from all years in that analysis.

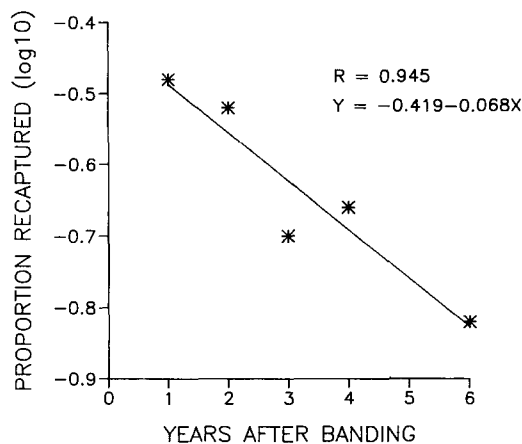


FIGURE 1. Regression of recapture rate on the time elapsed since banding (for data used see text).

RESULTS

The number of birds trapped annually ranged from 6–51, and the number recaptured from previous years ranged from 39–83% of those caught (Table 1). Survival estimates based on SURGE were 0.50 for the first year after capture and 0.88 for subsequent years ($P < 0.01$, Table 2). The estimate from the second and subsequent years gives an estimated life expectancy of 8.8 years.

The recapture probabilities estimated by SURGE varied from 0.11–0.65. The value for the lowest year (1990) was outside the 95% confidence limits for all other years. Only seven birds were trapped that year because catching conditions were poor on the two nights when trapping was attempted. Consequently, I omitted data from 1990 from the regression analysis. Using the other five years available yielded a regression coefficient of -0.068 (Fig. 1). This is equivalent to an annual survival of 0.86, with 95% confidence limits of 0.78–0.93. Life expectancy was estimated as 7.6 years.

DISCUSSION

The two methods used provide very similar estimates of annual survival (0.88, 0.86). This is not unexpected, as they are based largely on the same data set (the regression estimate refers only to the survival of birds banded in 1985 and 1986, whereas the SURGE estimate uses data from all years). The SURGE estimate incorporates more data and is probably more reliable. Both estimates are necessarily only minimum estimates, as the methods make no distinction between mortality and dispersal occurring if birds moved outside the capture area permanently during the course of the study. This constraint is inherent in most survival rate estimates based on population samples, rather than on entire colonies. However, auks rarely move their breeding site once they have begun to breed (Harris and Birkhead 1985).

Speich and Manuwal's (1974) survival estimate of 0.83 for Cassin's Auklets at the Farallon Islands falls within the 95% confidence interval for either of my

estimates. Taken together, the estimates from the two areas suggest that an adult annual survival rate between 0.8 and 0.9 may be normal for Cassin's Auklets, a somewhat lower survival rate than for the larger auks (Croxall and Gaston 1988).

The survival rate estimated here for Cassin's Auklets is significantly higher ($P < 0.05$) than the survival rate of 0.77 (95% confidence limits 0.67–0.84) estimated for Ancient Murrelets using the same procedures (Gaston 1990). The mean estimates derived from SURGE for the two species in the Queen Charlotte Islands suggest that Cassin's Auklets exhibit a life expectancy almost double that of the sympatric Ancient Murrelets (8.8 compared to 4.8 years). This supports my contention that the survival of adult Ancient Murrelets is exceptionally low for a pelagic marine bird, and that this may be linked to the precocial departure strategy of their chicks (Gaston 1990).

I thank Alan Burger, Ian Jones, Andrea Lawrence, David Noble, David Powell, Steven Smith, and the volunteers of the Laskeek Bay Conservation Society for their help with the field work involved in this project.

LITERATURE CITED

- AINLEY, D. G., AND R. J. BOEKELHEIDE. 1990. Seabirds of the Farallon Islands. Stanford Univ. Press, Stanford, CA.
- CLOBERT, J., LEBRETON, J. D., AND ALLAINE, D. 1987. A general approach to survival rate estimation by recaptures or resightings of marked birds. *Ardea* 75:133–142.
- CROXALL, J. P., AND A. J. GASTON. 1988. Patterns of reproduction in high-latitude northern- and southern-hemisphere seabirds. *Proc. Int. Orn. Cong.* 19: 1176–1194.
- FURNESS, R. W. 1978. Movement and mortality rates of Great Skuas ringed in Scotland. *Bird Study* 25: 229–238.
- GAILLARD, J.-M., D. PONTIER, D. ALLAINE, J. D. LEBRETON, J. TROUVILLIEZ, AND J. CLOBERT. 1989. An analysis of demographic tactics in birds and mammals. *Oikos* 56:59–76.
- GASTON, A. J. 1990. Population parameters of the Ancient Murrelet. *Condor* 92:998–1011.
- HARRIS, M. P., AND T. R. BIRKHEAD. 1985. Breeding ecology of the Atlantic Alcidae, p. 155–204. *In* D. N. Nettleship and T. R. Birkhead [eds.], *The Atlantic Alcidae*. Academic Press, London.
- LEBRETON, J. D., AND J. CLOBERT. 1986. User's manual for program SURGE. Centre National de Recherche Scientifique, Montpellier, France.
- NELSON, D. A. 1991. Demography of the Pigeon Guillemot on Southeast Farallon Island, California. *Condor* 93:768–773.
- RODWAY, M. S., M. J. F. LEMON, AND G. W. KAISER. 1988. British Columbia seabird colony inventory: report #1—East coast Moresby Island. Tech. Rep. Ser. No. 50. Can. Wildl. Serv., Pacific and Yukon Region. Vancouver, British Columbia.
- SPEICH, S., AND D. A. MANUWAL. 1974. Gular pouch development and population structure in Cassin's Auklet. *Auk* 91:291–306.