

- Ph.D. dissertation, Univ. Minnesota, Minneapolis.
- CALDWELL, G. S., AND R. W. RUBINOFF. 1983. Avoidance of venomous sea snakes by naive herons and egrets. *Auk* 100:195-198.
- COPPINGER, R. P. 1969. The effect of experience and novelty on feeding behavior with reference to the evolution of warning coloration in butterflies. I. Reactions of wild-caught adult Blue Jays to novel insects. *Behaviour* 35:45-60.
- GWINNER, E. 1964. Untersuchungen über das Ausdrucks- und Sozialverhalten des Kolkraben (*Corvus corax* L.). *Z. Tierpsychol.* 21:657-748.
- HEINRICH, B. 1988a. Winter foraging at carcasses by three sympatric corvids, with emphasis on recruitment by the raven, *Corvus corax*. *Behav. Ecol. Sociobiol.* 23:141-156.
- HEINRICH, B. 1988b. Why do ravens fear their food? *Condor* 90:950-952.
- HEINRICH, B. 1989. Ravens in winter. Summit Books of Simon & Schuster, New York.
- HEINRICH, B. 1995. Neophilia and exploration in juvenile Common Ravens, *Corvus corax*. *Anim. Behav.* 50:695-704.
- JAMES, F. C. 1971. Ordinations of habitat relationships among breeding birds. *Wilson Bull.* 83:215-235.
- MARZLUFF, J. 1988. Do Pinyon Jays alter nest placement based on prior experience? *Anim. Behav.* 36:1-10.
- MARZLUFF, J., AND B. HEINRICH. 1991. Foraging by Common Ravens in the presence and absence of territory holders: An experimental analysis of social foraging. *Anim. Behav.* 42:755-770.
- ROPER, T. J. 1990. Responses of domestic chicks to artificially coloured insect prey: Effects of previous experience and background colour. *Anim. Behav.* 39:466-473.
- SCHULER, W., AND E. HESSE. 1985. On the function of warning coloration: A black and yellow pattern inhibits prey-attack by naive domestic chicks. *Behav. Ecol. Sociobiol.* 16:249-255.
- SMITH, S. M. 1975. Innate recognition of coral snake pattern by a possible avian predator. *Science* 187:759-760.
- STIEHL, R. B. 1978. Aspects of the ecology of the Common Raven in Harney Basin, Oregon. Ph.D. dissertation, Portland State Univ., Portland, Oregon.

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Survival Rates of Puerto Rican Birds: Are Islands Really That Different?

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The comparison of tropical birds having small clutches and long lifespans with temperate birds having large clutches and short lifespans is one of the cornerstones of theories dealing with avian reproductive strategies (Cody 1966, 1971, Stearns 1976, Ricklefs 1983, 1992, Murray 1985, Skutch 1985, Godfray et al. 1991). Karr et al. (1990) described the limited data supporting the assumption of long tropical lifespans and provided data for one sample of tropical birds—25 species from Panama—that did not show greater survivorship than a sample of temperate species (10 from Maryland). Their paper provides one of the first comparisons of long-term data from sets of species from two regions with survival rate estimates computed using capture-recapture models developed in recent years to permit inferences unconfounded by sampling probabilities (Pollock et al. 1990).

To better understand whether regional differences

in avian survival rates occur, more mark-recapture data are needed for analysis using the above models. Here, we offer a long-term data set on the survivorship of 12 species of Puerto Rican birds computed with the models used by Karr et al. (1990). We compare these data and other known demographic traits of resident Puerto Rican species living in a dry-forest community with those of Karr et al. (1990) for Panama and Maryland, and suggest how the Puerto Rico data comply with common assumptions about tropical birds. We recognize that only with the accumulation of many such data sets from all areas can one confidently generalize about the demographic traits upon which so many evolutionary models rest.

Study area and methods.—Our studies were done within the Guanica State Forest in southwestern Puerto Rico. This 4,000-ha tract of subtropical deciduous forest has been protected by the Commonwealth of

Puerto Rico for 60 years and is designated a World Biosphere Reserve. About one-half of the forest is in a relatively natural state, while the other half is in various stages of regeneration. Our long-term study site was near the center of the forest in an undisturbed area (for a full description and photographs, see Terborgh and Faaborg 1973). This very seasonal environment receives an average annual rainfall of about 35 cm with a pronounced December–April dry season. Two severe droughts occurred during our sampling period; total populations dropped to about one-third their peak levels in association with these droughts (Faaborg et al. 1984, Faaborg and Arendt 1992).

We sampled bird populations using mist nets placed end-to-end in a straight line through forest vegetation. The data analyzed here come from a 16-net line that had been operated at least once a year (but no more than twice) for the period 1973–1990 except for 1977 and 1979. Nets were operated from dawn to dusk for three consecutive days in early January or early February, with occasional additional samples in June or October. All birds captured were banded (or the band number recorded if the bird had been previously banded), weighed, measured, and released.

Estimates of survival rates were made from capture-recapture models using the program JOLLY as described by Pollock et al. (1990). This program contains analyses for as many as four models with varying assumptions about rates and characteristics of mortality, immigration/emigration, and capture probability. For most species, model D was the best estimator, as it was for the data analyzed by Karr et al. (1990). Both survival rate and capture probability are assumed constant per unit time in model D. Model A was the best fit for two species; this is the standard Jolly-Seber model permitting time-specific capture probability and survival probability (Jolly 1965, Seber 1965).

Although 24 species of resident Puerto Rican birds were banded over the 18-year period of study, only 9 species had samples large enough to compute estimates of survival rate. The others were either captured infrequently or rarely showed recaptures in the study site. Three additional winter-resident species (birds that breed in North America, but spend up to eight months in Puerto Rico) were recaptured frequently enough to use with the models.

Results.—Average survival rates were estimated for nine resident Puerto Rican species and three winter resident species (Table 1). The average survival rate estimate for the resident species ($\bar{x} = 0.68 \pm \text{SE}$ of 0.04) is significantly different from that shown by Karr et al. (1990) for birds of Panama ($\bar{x} = 0.56 \pm 0.02$; $t = 2.943$, $df = 32$, $P < 0.005$) and Maryland ($\bar{x} = 0.54 \pm 0.03$; $t = 2.968$, $df = 17$, $P < 0.005$; Fig. 1). Three Puerto Rican species have survival-rate estimates greater than any of the 25 Panamanian species, and only 2 Puerto Rican species have survival rate esti-

TABLE 1. Survival rate data for birds banded at Guanica Forest, Puerto Rico, 1973–1990.

Species	Number of		Captures/individual	Probability of capture	Model	Annual survival rate ($\pm \text{SE}$)
	Captures	Individuals				
Residents						
Puerto Rican Tody (<i>Todus mexicanus</i>)	61	43	1.42	0.21	D	0.68 ± 0.07
Puerto Rican Flycatcher (<i>Myiarchus antillarum</i>)	98	62	1.58	0.20	D	0.79 ± 0.04
Caribbean Elaenia (<i>Elaenia martinica</i>)	124	107	1.16	0.10	D	0.72 ± 0.10
Pearly-eyed Thrasher (<i>Margarops fuscatus</i>)	158	124	1.27	0.10	D	0.77 ± 0.10
Red-legged Thrush (<i>Turdus plumbeus</i>)	83	59	1.41	0.14	D	0.78 ± 0.05
Puerto Rican Vireo (<i>Vireo latimeri</i>)	33	19	1.74	0.29	D	0.68 ± 0.08
Adelaide's Warbler (<i>Dendroica adelaidae</i>)	88	72	1.22	0.32	A*	0.55
Bananaquit (<i>Coereba flaveola</i>)	402	348	1.16	0.31	A*	0.51
Puerto Rican Bullfinch (<i>Loxigilla portoricensis</i>)	316	248	1.27	0.15	D	0.64 ± 0.04
Winter residents						
Black-and-white Warbler (<i>Mniotilta varia</i>)	77	57	1.35	0.28	D	0.59 ± 0.07
Ovenbird (<i>Seiurus aurocapillus</i>)	33	28	1.18	0.27	D	0.43 ± 0.13
American Redstart (<i>Setophaga ruticilla</i>)	86	67	1.28	0.23	D	0.56 ± 0.07

* No standard error computed with model A because some of annual survival estimates have undefined standard errors.

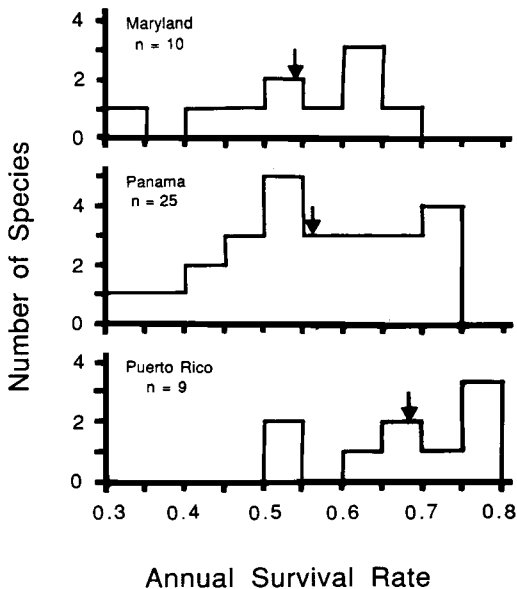


Fig. 1. Distribution of survival-rate estimates for Puerto Rican resident birds (our data) compared to similar estimates for species from Panama and Maryland (data from Karr et al. 1990). The mean estimated survival rate for each location's population shown by arrow.

mates as low as the average for the species in the Panama and Maryland data sets. The three winter-resident species had an average annual survival rate of 0.54 (Table 1), which is almost exactly the same as the average annual survival-rate values suggested by Karr et al. (1990) for temperate residents and Nichols et al. (1981) for estimates calculated for the same or similar migratory species on their breeding grounds.

Model D provided the best estimator for all but two of the resident species and all of the winter residents (Table 1). The two species for which model A was the best fit also had the lowest survival-rate estimates. One of these, the Bananaquit, was the most abundant species prior to the severe drought of 1973–1977, with as many as 53 captures per three-day netting period. Because model A computes annual estimates of survival rate between sampling periods, we can compare survival-rate estimates during the drought with those of more typical periods. These annual estimates of survival rate averaged 0.37 during the first five samples, when drought conditions were most pronounced, but they averaged 0.77 during the last five years (1985–1990), a more favorable period climatically. The Adelaide's Warbler also fits model A, but it was always captured at a low frequency, and there were few enough captures during the drought period that the model could make no annual estimates in some years.

Discussion.—Average survival-rate estimates for the nine Puerto Rican resident birds analyzed here are greater than those computed by similar methods for species from Maryland and Panama (Karr et al. 1990). A recent study in Puerto Rico also computed an average annual survival rate for the Zenaida Dove (*Zenaida aurita*) of 0.84 ± 0.06 using model A (Milan Rivera unpubl. data). A comparison of these 10 resident species of Puerto Rico and 10 species from Maryland (Karr et al. 1990) fits the widely held assumption of higher survival rates in tropical birds than temperate species. The higher survival rates of Puerto Rican than Panamanian bird species is more paradoxical, particularly given that we are comparing a very seasonal location (Guanica, Puerto Rico) with forests that are more mildly seasonal (lowland Panama; see Leigh et al. 1982). General theory would predict the opposite pattern of survival.

Are there characteristics of the Puerto Rican species sampled in this study that might explain this discrepancy? Two of the Puerto Rican species (the Pearly-eyed Thrasher at 100 g, and Red-legged Thrush at 75 g) are larger in size than any of the Panamanian species sampled; large species tend to be abundant in island communities (Terborgh et al. 1978, Faaborg 1985) and, typically, are assumed to have higher survival rates than smaller species. Yet, deleting these from Figure 1 still leaves the remaining Puerto Rican species clustered at the high end of the range of values for Panamanian species. These remaining species tend to be relatively small (5–32 g), but otherwise are typical of the land-bird fauna of the West Indies. Included are such common genera as *Dendroica*, *Vireo*, *Elaenia*, *Loxigilla*, *Myiarchus*, and *Coereba*.

If these high survival-rate estimates are accurate, commonly held ideas about reproductive strategies suggest that Puerto Rican birds should have relatively small clutches. Yet, the average clutch size of the nine resident species is three eggs (Bond 1985), with a range of two to five. This compares to the two- or three-egg clutches laid by the Panamanian species and three- to six-egg clutches of the Maryland species (Karr et al. 1990).

Although the general relationship between survival rates and clutch size has been proposed for a long time, a variety of other mechanisms affecting the evolution of clutch size has also been presented (for review, see Godfray et al. 1991). Factors such as length of breeding season, nest-predation rates, and seasonality of food supply may affect the evolution of clutch size, but seldom in easily discernable ways.

For example, most Guanica birds appear to have a fairly limited breeding season (Wetmore 1916, Bond 1943), as they will not initiate nesting until after rains end the dry season in April or May (pers. obs.). Residents appear to stop breeding in July or early August, although rainfall levels actually increase in August and September. It is not known whether this cessation of breeding reflects the effects of competition with

winter residents, which appear in large numbers in September and October, or the fact that young produced so late in the breeding season may have little chance of surviving the dry season (for discussion, see Faaborg et al. 1984). It does suggest that Puerto Rican residents have little chance for intraseason bet-hedging strategies, which have been suggested as allowing tropical species to lay several small clutches through the breeding season, rather than risking large amounts of energy on a single, large clutch (Moreau 1944, Foster 1974, 1975). Rather, Puerto Rican dry-forest species have breeding seasons not unlike those of temperate species in length, with limited numbers of chances to successfully produce a clutch.

Although the seasonal environment may limit the breeding season at Guanica, it probably also provides abundant food for breeding birds as the forest becomes green following the first rains that end the dry season (Janzen 1973). Such a burst of production might be found in Maryland, but may be less pronounced in Panama. Such seasonality of resource abundance would match Ashmole's hypothesis (Ashmole 1963, Ricklefs 1980), which suggests that clutch size is a function of differences between resource availability during the breeding and nonbreeding seasons. In this case, the burst of productivity at Guanica that follows the rains would allow parents to feed a large clutch more easily than in Panama, where such a large burst may not occur. Ricklefs (1980) also has suggested that the departure of the great densities of wintering birds in the Greater Antilles may allow residents there to lay larger clutches through competitive release. Lesser Antillean species, which do not have to deal with high densities of winter residents, lay smaller clutches than Greater Antillean residents, but they also have longer breeding seasons (Bond 1985).

Predation also has been judged to be important to the evolution of clutch size (Martin 1987). Few species of nest predators live at Guanica, and these are generally uncommon, presumably reducing the risk factor associated with nesting there compared to Panama (although recent work on the Puerto Rican Vireo shows high losses of nests to predators in Guanica [Woodworth pers. comm.]).

Using standard ideas in life-history trade-offs, both the lack of nest predators and the seasonally variable food supply found in the Guanica Forest would favor larger clutches than in an area with greater predation and a seasonally more uniform food supply. The limited breeding season relative to other tropical locations might also favor larger clutches. The apparently high survival rates of Guanica birds suggest that clutch sizes equivalent to those of Maryland are not needed to simply replace mortality. At some point, natural selection on offspring quality should work to limit clutch size if local populations become saturated, particularly if reduced clutch size increases an offspring's chances of making it through its first dry season.

A cursory comparison of avian demography in

Puerto Rico and Panama suggests that a simple trade-off between high survival rates and small clutch size may not be at work in the tropics in general. If the Panama data reflect the general situation in the tropics, it appears that Panamanian birds must compensate for their relatively high mortality rates in small increments, either because they balance high nest predation with repeated nesting attempts during their extended potential breeding season, or because high fledgling survival puts a premium on producing fewer, high-quality young. This contrasts with the long survival times plus large clutches of Puerto Rican residents. Karr et al. (1990) noted that most examples of long-lived birds come from islands; is it possible that there is something distinctively different about island populations that we do not yet understand?

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LITERATURE CITED

- ASHMOLE, N. P. 1963. The regulation of numbers of tropical oceanic birds. *Ibis* 103:458-478.
- BOND, J. 1943. Nidification of the passerine birds of Hispaniola. *Wilson Bull.* 55:115-125.
- BOND, J. 1985. *Birds of the West Indies*. Collins, London.
- CODY, M. L. 1966. A general theory of clutch size. *Evolution* 20:174-184.
- CODY, M. L. 1971. Ecological aspects of reproduction. *Avian Biol.* 1:461-512.
- FAABORG, J. 1985. Ecological constraints on West Indies bird distributions. Pages 621-653 in *Neotropical ornithology* (P. A. Buckley, M. S. Foster, E. S. Morton, R. S. Ridgely, and F. G. Buckley, Eds.). *Ornithol. Monogr.* 36.
- FAABORG, J., W. J. ARENDT, AND M. S. KAISER. 1984. Rainfall correlates of bird population fluctuations in a Puerto Rican dry forest: A nine year study. *Wilson Bull.* 96:575-593.
- FAABORG, J., AND W. J. ARENDT. 1992. Rainfall correlates of bird population fluctuations in a Puerto

- Rican dry forest: A 15-year study. *Ornitologia Caribena* 3:10-19.
- FOSTER, M. S. 1974. A model to explain molt-breeding overlap and clutch size in some tropical birds. *Evolution* 28:182-190.
- FOSTER, M. S. 1975. The overlap of molting and breeding in some tropical birds. *Condor* 77:304-314.
- GODFRAY, H. C. J., L. PARTRIDGE, AND P. H. HARVEY. 1991. Clutch size. *Annu. Rev. Ecol. Syst.* 22:409-429.
- JANZEN, D. H. 1973. Sweep samples of tropical foliage insects: Effects of seasons, vegetation types, elevation, time of day, and insularity. *Ecology* 54:687-708.
- JOLLY, G. M. 1965. Explicit estimates from capture-recapture data with both death and immigration-stochastic models. *Biometrika* 52:225-247.
- KARR, J. R., J. D. NICHOLS, M. K. KLIMKIEWICZ, AND J. D. BRAWN. 1990. Survival rates of birds of tropical and temperate forests: Will the dogma survive? *Am. Nat.* 136:277-291.
- LEIGH, E. G., A. S. RAND, AND D. M. WINDSOR (Eds.). 1982. *The ecology of a tropical forest*. Smithsonian Institution Press, Washington, D.C.
- MARTIN, T. E. 1987. Artificial nest experiments: Effects of nest appearance and type of predator. *Condor* 89:925-928.
- MOREAU, R. E. 1944. Clutch size: A comparative study, with reference to African birds. *Ibis* 86:286-347.
- MURRAY, B. G., JR. 1985. Evolution of clutch size in tropical species of birds. Pages 505-519 in *Neotropical ornithology* (P. A. Buckley, M. S. Foster, E. S. Morton, R. S. Ridgely, and F. G. Buckley, Eds.). *Ornithol. Monogr.* 36.
- NICHOLS, J. D., B. R. NOON, S. L. STOKES, AND J. E. HINES. 1981. Remarks on the use of mark-recapture methodology in estimating avian population size. Pages 121-136 in *Estimating numbers of terrestrial birds* (C. J. Ralph and J. M. Scott, Eds.). *Stud. Avian Biol.* 6.
- POLLOCK, K. H., J. D. NICHOLS, C. BROWNIE, AND J. E. HINES. 1990. *Statistical inference for capture-recapture experiments*. *Wildl. Monogr.* 107.
- RICKLEFS, R. E. 1980. Geographical variation in clutch size among passerine birds: Ashmole's hypothesis. *Auk* 97:38-49.
- RICKLEFS, R. E. 1983. Comparative avian demography. *Curr. Ornithol.* 1:1-32.
- RICKLEFS, R. E. 1992. The megapopulation: A model of demographic coupling between migrant and resident landbird populations. Pages 537-548 in *Ecology and conservation of Neotropical migrant landbirds* (J. M. Hagan III and D. W. Johnston, Eds.). Smithsonian Institution Press, Washington, D.C.
- SEBER, G. A. F. 1965. A note on the multiple-recapture census. *Biometrika* 52:249-259.
- SKUTCH, A. F. 1985. Clutch size, nesting success, and predation on nests of Neotropical birds, reviewed. Pages 575-594 in *Neotropical ornithology* (P. A. Buckley, M. S. Foster, E. S. Morton, R. S. Ridgely, and F. G. Buckley, Eds.). *Ornithol. Monogr.* 36.
- STEARNS, S. C. 1976. Life-history tactics: A review of the ideas. *Q. Rev. Biol.* 51:3-47.
- TERBORGH, J., AND J. FAABORG. 1973. Turnover and ecological release in the avifauna of Mona Island, Puerto Rico. *Auk* 90:759-779.
- TERBORGH, J., J. FAABORG, AND H. J. BROCKMAN. 1978. Island colonization by Lesser Antillean birds. *Auk* 95:59-72.
- WETMORE, A. 1916. *Birds of Puerto Rico*. U.S. Dep. Agric. Bull. 326.

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