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THE EVOLUTION OF PASSERINE LIFE HISTORIES ON OCEANIC ISLANDS, AND ITS IMPLICATIONS FOR THE DYNAMICS OF POPULATION DECLINE AND RECOVERY

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Abstract. The Seychelles Archipelago in the Indian Ocean lies a few degrees south of the equator, about 1,600 km east of Kenya. The Galápagos Archipelago in the Pacific Ocean lies on the equator about 1,000 km west of Ecuador. The Hawaiian Islands straddle the Tropic of Cancer and are about 3,500 km southwest of California. The Seychelles Warbler (*Acrocephalus sechellensis*) has a long life, usually begins breeding at age four, lays a one-egg clutch, and is single brooded (a combination that is extraordinary for a small passerine). In contrast, the Large Cactus Finch (*Geospiza conirostris*) of the Galápagos has a short life (some cohorts live no more than seven years), usually begins breeding at age one (but some may begin at age two or three), lays a large clutch (about four eggs), and successfully rears as many as six broods per year (occasionally, it rears none). The life history of Hawaiian passerines appears to be intermediate between these extremes. These differences are attributable to environmental differences affecting the length of the breeding season, survivorship, and reproductive success.

Many island populations are threatened with extinction because of introduced disease, such as avian malaria, and predators, such as rats, cats, and humans, as well as destruction of their habitats by introduced animals, such as goats, and by humans. Island populations are at greater risk of serious population decline than mainland populations because of the limited amount of habitat and because they have evolved a small biotic potential (r_{max}). The small biotic potential results from the evolution of long life expectancy and small clutch size in environments that were virtually predator- and disease-free prior to their discovery by the human species. Conservation of endemic island populations will require, at least, the preservation of suitable habitat and control of predator and disease organisms.

Key Words: age of first breeding; biotic potential, breeding season; clutch size; demography; Galápagos; Hawai'i; life history; population dynamics; r_{max}; Seychelles; survival.

Clutch-size variations in birds are well-known, the most prominent of which is the increase in clutch size with increasing latitude (Lack 1947, 1948; Cody 1966, 1971; Klomp 1970). Clutch size also tends to be smaller on oceanic islands than on the nearest mainland in the temperate zone, but not in the tropics, where clutch size is about the same on islands and on the adjacent mainland (Lack 1968, Cody 1971). On oceanic islands within the tropics, however, clutch size in passerines varies from one egg in the long-lived, single-brooded Seychelles Warbler (*Acrocephalus sechellensis*) to four eggs in the short-lived, multibrooded Large Cactus Finch (*Geospiza conirostris*). In this paper I explore the evolution of life-history variations of passerines on tropical oceanic archipelagos.

The theory on the evolution of clutch size, proposed to explain this variation in life histories among passerines on oceanic archipelagos, will be used to explore the evolution of a species' biotic potential (i.e., r_{max}), that is, its maximum rate of increase in natural habitat in uncrowded conditions. A species' biotic potential is a measure of the rate of recovery of a population when the environment is managed for that population.

THE BIRDS

The Seychelles Warbler is endemic to Cousin Island in the Seychelles Archipelago in the western Indian Ocean. In 1959 the global population of Seychelles Warbler numbered 26 individuals, and in 1968 the International Council for Bird Preservation undertook management of the island for the preservation of the species. Because the coconut palms (*Cocos nucifera*) were prevented from regenerating and the indigenous vegetation was allowed to flourish, the warbler population grew to over 300 birds by 1982 (Komdeur 1994a). In 1988, 29 birds were transferred to Aride Island, and in 1990 another 29 were transferred to Cousine Island. Both introductions have been successful (Komdeur 1994a).

On Cousin Island, the Seychelles Warbler is long-lived with an annual adult survival rate of 0.82 (Table 1). One bird survived to its 28th year (S. Dykstra, pers. comm.). Females begin breeding at age four and rarely lay more than one one-egg clutch per year (Komdeur et al. 1995, 1997). On Aride and Cousine islands, where the populations are still growing, females begin breeding at age one, lay a larger clutch, and often rear more than one brood per year (Komdeur 1994a, 1996).

The life history of the Large Cactus Finch on Isla Genovesa in the Galápagos Archipelago (Grant and Grant 1989) is strikingly different from that of the Seychelles Warbler (Table 1).

TABLE 1. LIFE-HISTORY CHARACTERISTICS OF FIVE PASSERINE SPECIES FROM THREE OCEANIC ARCHIPELAGOS

	Seychelles Warbler[a]	Palila[b]	Hawai'i 'Ākepa[c]	'Ōma'o[d]	'Elepaio[e]	Large Cactus Finch[f]
Age of first breeding	4	3 (males) 1–2 (females)	2 (males) 1 (females)	—	1	1–3
Mean clutch size	1	1.9	2–3	1–2	2	3.5
Maximum broods per year	1	3	1	—	2	0–6
Breeding season length (mo)	12	6–7	4	12 (peak May–July)	3	0–6
Survival of fledglings	0.44	0.36	0.43	0.40	—	0.10
Adult survival	0.81	0.65 (males) 0.62 (females)	0.83 (males) 0.80 (females)	0.66	0.88 (males) 0.80 (females)	0.62[g]

[a] Komdeur (1992, 1994a), Komdeur et al. (1997).
[b] van Riper (1980a), Lindsey et al. (1995), T. K. Pratt (pers. comm.).
[c] Lepson and Freed 1995, L. A. Freed (pers. comm.).
[d] Berger (1981), Ralph and Fancy (1994c).
[e] van Riper (1995), Vander Werf (unpubl. abstract).
[f] Grant and Grant (1989).
[g] See text.

Females usually begin breeding at age one or two, but some females do not breed until age three, and lay a modal clutch size of four eggs. Annual variation in number of clutches laid varies greatly, from zero in severe drought years to as many as seven in wet years (see Fig. 4.6 in Grant and Grant 1989). Consistent with high reproduction is the short life of Large Cactus Finches, four of five reported cohorts of females surviving no more than seven years (males tend to survive longer, one cohort of males surviving beyond ten years). About 10% of fledglings survive their first year (see Tables 3.1 and 3.2 in Grant and Grant 1989). Although Grant and Grant (1989, Table 3.2) use subsamples to give estimates of annual adult survival for males of 0.81 and for females of 0.78, the largest sample (1,244 banded birds known to have fledged in the years 1978 to 1983) gives an annual adult survival of 0.50. This is probably an underestimate (with annual adult survival of 0.50, we should expect to see 1 in 1,000 reach age eight). Annual adult female survival may be closer to 0.62 (Table 3.2 in Grant and Grant 1989). With this survival rate, we should expect 1 in 1,000 females to reach age ten). This may also be an underestimate (P. R. Grant, pers. comm.). Annual adult female survival of 0.78, however, is too great (1 in 1,000 expected to reach age 19).

The life histories of the Medium Ground Finch (*Geospiza fortis*) and Common Cactus Finch (*Geospiza scandens*) on Isla Daphne Major are similar to that of the Large Cactus Finch (Grant and Grant 1992). Most females begin breeding between ages one and three. One of four cohorts (1975, sexes combined) of each species survived to age 15 (*G. fortis*) and 16 (*G. scandens*), and the 1978 cohorts had three (*G. scandens*) and five (*G. fortis*) survivors at age 13. However, there was no cohort of *G. fortis* produced in 1977, and the 1976 cohort had only one bird survive two years. One cohort (1977) of *G. scandens* did not survive three months, and another (1976) had one bird survive two years. Although adult survivorship appears to be high (about 80%) in some cohorts, the mean life expectancy of the average bird from the time of its being laid as an egg is short. Females of both species lay a modal clutch of four eggs (Grant and Grant 1989).

The Seychelles Warbler and the *Geospiza* finches seem to represent extremes in the evolution of life histories on tropical oceanic islands. The Seychelles Warbler has a long life and low reproductive rate, whereas the *Geospiza* finches have short life expectancies and high reproductive rates.

Intermediate are the indigenous Hawaiian passerines (Table 1). For example, the Palila (*Loxioides bailleui*) has a clutch size of 1.9 (van Riper 1980a). Females begin breeding at age one or two and rear at most three broods in a season (T. K. Pratt, pers. comm.). Survivorship of fledglings is 0.36, and annual adult survivorship is 0.63 (Lindsey et al. 1995a). T. K. Pratt et al. (unpubl. data) found a small difference in survivorship between males and females, 0.65 and 0.62, respectively.

In other Hawaiian passerines, clutch size varies between two in the Po'ouli (*Melamprosops phaeosoma*; Pratt et al. 1997b) and 'Elepaio (*Chasiempis sandwichensis*; van Riper 1995, VanderWerf 1998a) and 3.2 in the Laysan Finch (*Telespiza cantans*; Morin 1992a). Adult survivorship varies between 0.55 in the 'I'iwi (*Vestiaria coccinea*; Ralph and Fancy 1995), 0.80 for female and 0.83 for male Hawai'i 'Ākepa (*Loxops coccineus*; Lepson and Freed 1995), and

0.78 for female and 0.87 for male 'Elepaio (VanderWerf 1998a). Most females produce at most a single brood a year. Unfortunately, survivorship from the laying of the egg through the first year is poorly known in all these species.

THE ENVIRONMENTS

The granitic central islands of the Seychelles Archipelago are the remains of the breakup of Gondwanaland. The climate is relatively benign (Court 1992). The drier southeast monsoon occurs from May through October, and the wetter northwest monsoon occurs between December and March. The mean annual precipitation of 1,500 to 2,200 mm is distributed throughout the year, varying from 61 and 64 mm in June and July to 296 and 387 mm in December and January (at Point La Rue international airport; Court 1992). Temperature varies slightly, from a mean low of 23.9° C in December to a mean high of 31.3° C in April (Court 1992).

Although the availability of food and the probability of success in rearing young from a breeding attempt varied considerably, some breeding activity (nest building, incubation, and feeding of young) on Cousin and Cousine islands occurred throughout the year (Komdeur 1994a, 1996; Komdeur et al. 1995). On Aride Island, where the Seychelles Warbler has recently been introduced, some breeding activity occurred in almost 100% of territories in every month of the year.

In contrast, the climate of the volcanic Galápagos Archipelago is more variable, severe, and unpredictable, especially with regard to rainfall (Grant and Boag 1980, Grant 1986, Grant and Grant 1989). Normally, a warm wet period from about January to May is followed by a cool dry period from about June to December, in response to the annual north-south movements of the southern, cooler Humboldt Current and the warmer, tropical current flowing from the Gulf of Panama. Temperature varies between a mean high of about 30° C in March to a mean low of about 19° C in September at the Charles Darwin Research Station. According to Grant (1986:25), "The most striking feature of the Galápagos climate is the extraordinary year-to-year variation in rainfall." During the wet season, rainfall varies from completely absent (in 1985) to quite heavy (116 mm in February 1980, compared with a mean precipitation of about 18 mm per month from January to May in years without El Niño rainfall; Grant and Grant 1989). Superimposed on these variations are El Niño-Southern Oscillation (ENSO) events, which occur every 2 to 11 years (averaging 7 years). At these times precipitation can be very heavy, even during the "dry" season (e.g., 505 mm on Isla Genovesa in July 1983; Grant and Grant 1989). Nevertheless, the average monthly rainfall during the wet season in the Galápagos (55 mm from 1978 through 1988; Grant and Grant 1989) is considerably less than the mean monthly low during the five drier months of the southeast monsoon at the Seychelles (91 mm from May through September; Court 1992).

The food supply for the finches varies with the amount of rainfall (Grant and Grant 1989), and thus breeding activity of the birds is extraordinarily variable. During drought years, breeding may not occur at all, and during wet years breeding may continue for seven to eight months, during which females may lay as many as seven clutches and rear as many as six broods (Grant and Grant 1989).

Lying about 20° north of the equator, the "Hawaiian Islands are justly famous for mild, uniform, subtropical weather . . . " (Carlquist 1970: 63). The northeast trade winds blow throughout most of the year (averaging about 300 days), and the difference between the mean summer (May to October) and mean winter (November to April) temperature is only 4° C. During the winter the wind sometimes shifts to the south (Kona winds), bringing hotter, stickier weather. Rain falls throughout the year but varies considerably between leeward and windward sides and with elevation. Hilo, on the island of Hawai'i, is the wettest city in the United States (3,300 mm per year), whereas on the leeward side of the islands rainfall may be as little as 250 mm.

Despite the year around near uniformity of the climate, the length of the breeding season of the endemic passerines varies from as short as two months (Po'ouli; Pratt et al. 1997b) to year-round ('Ōma'o [*Myadestes obscurus*]; Ralph and Fancy 1994c).

DISCUSSION

THE EVOLUTION OF CLUTCH SIZE

The clutch size of birds on oceanic islands tends to be smaller than on the nearest mainland in the temperate zone and about the same size in the tropics (Cody 1966, Lack 1968). The clutch sizes of Galápagos finches are exceptional in being larger than those of passerine species on the Santa Elena Peninsula of Ecuador (Marchant 1960), which in turn are larger than typical for tropical species (Marchant 1960, Cody 1966, Lack 1968, Skutch 1985). The clutch size of the Seychelles Warbler is exceptional in being the smallest for a passerine species.

If we are to understand the evolution of life-history variations, we must keep three facts in mind. First, the relationship between clutch size and other demographic parameters is given by the clutch-size equation (Murray and Nolan 1989),

$$C = \frac{a+1}{\sum_{\alpha}^{\omega} \lambda_x \sum_{1}^{n} P_i}, \quad (1)$$

where a is the primary sex ratio (assumed to be one in birds), λ_x is the probability of surviving from birth (in birds, from the laying of the egg) to age class x of those individuals from successful clutches or litters, α is the mean age class of first breeding, ω is the age class of last breeding, and $\Sigma_1^n P_i$ is the mean number of broods successfully reared during a breeding season. $\Sigma_1^n P_i = P_1 + P_2 + \ldots + P_n$, where P_1, P_2, and P_n are the probabilities of the females of a genotype successfully rearing at least one, two, and n broods during a breeding season. Furthermore, $P_1 + P_2 + \ldots + P_n = c_1 s_1 + c_2 s_2 + \ldots + c_n s_n$, where c_1, c_2, and c_n are the mean number of clutches laid in producing a first, second, and nth brood, and s_1, s_2, and s_n are the probabilities that first, second, and nth brood clutches produce at least one young to independence (Murray 1991a,b). Equation 1 must hold, regardless of one's explanation for the evolution of clutch size (Wootton et al. 1991, Murray 1992a).

With high quality data (large samples for almost 20 years), such as are available for the Florida Scrub-Jay (*Aphelocoma coerulescens*; Woolfenden and Fitzpatrick 1984), the equation works exceptionally well (Murray et al. 1989). The equation has been applied to data on only two other species, each producing a very good estimate of clutch size (Prairie Warbler [*Dendroica discolor*], Murray and Nolan 1989; House Wren [*Troglodytes aedon*], Kennedy 1991).

Second, if the probability of nest contents (eggs or nestlings) surviving from one day to the next is less than one, then smaller clutches always have a higher probability of having young leave the nest (s_i) than larger clutch sizes (Murray 1999). For example, a two-egg clutch always has a greater s_i than a three-egg clutch, and a four-egg clutch always has a higher s_i than a five-egg clutch because, in each case, the larger clutch always requires at least one more day to rear young to nest-leaving. The difference is small, but inasmuch as small differences may have big evolutionary effects (Fisher 1930), we should probably ask whether this small difference in survival of clutches of different size has evolutionary significance.

By "always" I am referring to a particular clutch laid by a particular female. I am not referring to a comparison between a five-egg clutch laid in May with a four-egg clutch laid in July, or a five-egg clutch laid by a female of one species with a four-egg clutch laid by a female of another species. If we are observing a female that has just laid a fourth egg in a clutch, we may ask, would she increase her probability of rearing any young from that clutch by laying an additional egg? The answer is, no. The only apparent exception: a female that lays two eggs and begins incubation with the first egg can do better than if she had laid one egg (Murray 1994a). If she began incubation with the second egg, however, s_i would be less than if she had laid one egg.

Third, it is important to understand that we cannot compare one or two components of a life history within, between, or among species and draw a conclusion about fitness (Murray 1992b, 1997a), much less make a prediction of what we should find in nature. We must consider the combination of factors explicit in Equation 1. For example, if annual adult survival is greater in one species than in another, we should not expect that it should necessarily have the smaller clutch. If juvenile survival of the first species were poorer than in the second, each species could have the same clutch size, or the first could have a larger clutch size. If age of first breeding were later in the first species than in the second, then each species could have the same clutch size, or the first could have a larger clutch size. In comparing species, we must be careful to control for or at least consider the possibility of multiple demographic differences between them.

With these constraints in mind, I have proposed that selection favors those females that lay as few eggs or bear as few young as are consistent with replacement because they have the highest probability of surviving to breed again, their young have the highest probability of surviving to breed, or both (Murray 1979, 1991a, 1999). What this means is that the genotype that has a clutch size that can replace itself has the greatest Malthusian parameter, the best measure of fitness (Murray 1992b, 1997a). Genotypes with clutch sizes smaller than replacement have negative Malthusian parameters because they are not producing enough young to replace themselves. Genotypes with larger clutch sizes have smaller Malthusian parameters than the replacement genotype because of the reduced reproductive success or survivorship imposed by the extra egg(s). This is a hypothesis that should be tested against empirical fact. So far, this hypothesis has led to several predictions that seem confirmed by the empirical evidence (Murray 1979, 1985, 1991a, 1999).

According to this hypothesis, selection favors the mean clutch size that just balances the im-

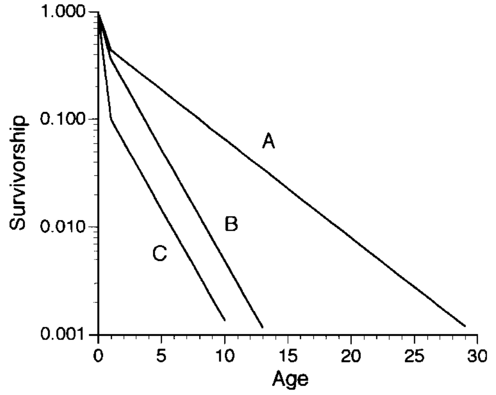

FIGURE 1. Survivorship curves for three species of passerines (data in Table 1). A = Seychelles Warbler, B = Palila, C = Large Cactus Finch.

pact of environmental factors affecting longevity (i.e., $\Sigma\lambda_x$) and the age of first breeding (i.e., α), both of which affect $\Sigma_\alpha^\omega\lambda_x$, and the probability of rearing young successfully from brood i (i.e., s_i, which affects $\Sigma_1^n P_i$). Such factors include the intensity of predation, disease, competition, and inclement weather, and the length of the breeding season. The latter especially affects $\Sigma_1^n P_i$. A long breeding season increases the number of opportunities (c_1) to rear a successful first brood (i.e., increasing P_1) and increases the probability of rearing several broods during a breeding season, increasing $\Sigma_1^n P_i$.

Unfortunately, the reported demographic data on the Seychelles Warbler, the Hawaiian passerines, and the Galápagos finches are not suitable for a rigorous comparative analysis. Data on one or more important parameters are usually lacking, based on small samples, or incorrectly calculated. Nevertheless, there are enough data (Table 1; Fig. 1) to support a preliminary analysis that may spur further investigation. Further investigation may change the numbers, but it probably would not change the interpretation.

Environmental conditions on the Seychelles certainly allow for a long life in the Seychelles Warbler. According to this hypothesis, selection should favor a small clutch size and few breeding attempts. Although the climate is suitable for breeding year-round on Cousin Island, where the population is limited by suitable breeding habitat, females normally lay only one egg per year. Furthermore, Seychelles Warblers live so long that initial breeding can be postponed, which in turn allows for the evolution of helpers at the nest (Komdeur 1992). On Aride and Cousine islands, however, where the species has recently been introduced, breeding often begins at age one, females often lay more than one egg per year, and, initially, young disperse to breeding territories rather than postpone breeding and act as helpers (Komdeur et al. 1995, Komdeur 1996).

In contrast, climatic variation on the Galápagos is so severe that life expectancy of the Large Cactus Finch at hatching is short (only about 10% survive the first year, whereas 10% of Palila survive to beyond age three and 10% of Seychelles Warbler to age eight [Fig. 1]), some females are forced to postpone breeding until suitable conditions occur, and in some years no breeding occurs at all. Under such conditions, the Galápagos finches must evolve a large clutch size and rear multiple broods when conditions favor breeding or become extinct.

The climate of the Hawaiian Islands is benign. Breeding may be year-round in some species (e.g., ‘Ōma‘o; Ralph and Fancy 1994c) but short in others, three to seven months in the ‘Elepaio (van Riper 1995) and only two months in the Po‘ouli (Pratt et al. 1997b). Nevertheless, breeding occurs each year, during which as many as two or three broods may be reared. Juvenile survivorship (0.36 in Palila and 0.40 in ‘Ōma‘o [Table 1]) is greater than in the Large Cactus Finch, but adult survivorship may be more typical of temperate zone birds (e.g., 0.62 in Palila and 0.66 in ‘Ōma‘o) or as great as in the Seychelles Warbler (e.g., 0.8 in female ‘Elepaio and Hawai‘i ‘Amakihi). An intermediate clutch size between those of the Seychelles Warbler and Large Cactus Finch is not surprising in these species.

The life histories of the passerines in the Seychelles, Galápagos, and Hawaiian islands seem consistent with the notion that the clutch size is adjusted to the population's life expectancy, age of first breeding, and probability of rearing one or more broods during a breeding season, which are constrained by environmental variables such as the intensity of predation, disease, competition, and inclement weather, and by the length of the breeding season.

Alternative hypotheses on the evolution of clutch size, such as Lack's hypothesis that the clutch size reflects the amount of food available for laying eggs and rearing young (Lack 1947, 1948, 1954, 1968) or the nest-predation hypothesis of Skutch (1949) and Martin (1992b), imply that the rest of a population's demographic characteristics are adjustments to the evolved clutch size. Thus, according to these hypotheses, populations with small clutch sizes, which have evolved in response to a limited food supply or to a high incidence of predation on nest contents, have evolved longer life (i.e., greater adult survivorship) or longer breeding seasons and multibroodedness. It is difficult to imagine how a population could evolve a longer life when lacking sufficient food for rearing a larger family or how a longer breeding season and multibroodedness could evolve in response to heavy predation on nest contents.

On the other hand, if reduced predation, disease, competition, and other sources of mortality result in increased longevity, and if s_i (the probability of rearing any young from a clutch) is greater for smaller clutches, then longer life should easily lead to the evolution of smaller clutches. If a population lives in a region that provides suitable conditions for breeding for much of the year (say, the tropics), it could evolve small clutches because s_i is greater for smaller clutches and females could lay more replacement clutches after failure (increasing c_i) and produce second, third, or more broods (increasing $\Sigma_1^n P_i$), whereas a population in a region with short breeding seasons (say, at higher latitudes), where few replacement clutches could be laid and no more than a single brood could be reared, should have a large clutch size.

It seems more likely that humans, whales, albatrosses, and the Seychelles Warbler have small litter and clutch sizes because they have evolved a long life, rather than because they have limited amounts of food available for rearing young or suffer high predation rates. It seems more likely that pigs, mice, phasianids, and the Large Cactus Finch have large litter and clutch sizes because they have a short life expectancy, rather than because they have access to a more abundant food supply or have fewer predators than longer lived species.

Equation 1 provides another clue. The only life history parameter that can be predicted from knowledge of the others is a population's mean clutch size. The other parameters of Equation 1, $\Sigma_\alpha^\omega \lambda_x$ and $\Sigma_1^n P_i$, are composites of two or more life history parameters, age-specific survivorship and age of first breeding in the former, and probability of rearing young from a clutch and number of clutches laid in rearing a brood in the latter. All kinds of life history combinations (of juvenile survival, adult survival, age of first breeding, single- or multibroodedness) may have the same clutch size. Philosophically, it seems more likely that the clutch size is a consequence of the evolution of the other life-history traits.

This study points out the need for high quality demographic data in evaluating evolutionary hypotheses. In order to predict clutch size from other demographic parameters, we need to know the number of clutches laid per female in rearing a first, second, or later brood (i.e., $c_1, c_2, \ldots, c_n$); the probability of rearing a first, second, or later brood from a clutch (i.e., $s_1, s_2, \ldots, s_n$); the mean age of first breeding (i.e., α); and annual survival rates (from which we calculate λ_x). In order to understand the evolution of clutch size, we will need to know further the influence of the factors affecting these parameters, such as the intensity of predation, disease, and competition, and the length of the breeding season (i.e., egg-laying season).

IMPLICATIONS FOR THE DYNAMICS OF POPULATION DECLINE AND RECOVERY

This analysis of clutch-size variations of island passerines is based on a conception of population dynamics different from that prevailing during the fifty years since Lack (1947, 1948, 1954, 1966) proposed that the clutch size reflected the maximum number of young the parents could rear on average and that the excess production was eliminated by density-dependent mortality, especially prior to the age of first breeding. This view was consistent with the older view of a population's "biotic potential" being kept in check by "environmental resistance" (Chapman 1928). Modifications to Lack's clutch-size hypothesis do not change the dynamics. Cody (1966) suggested that the clutch size was a function of the amount of energy available to the parents for reproduction, and Williams (1966) and Charnov and Krebs (1974) suggested that the clutch size was an "optimum," balancing the benefit of current reproduction against the costs of decreased future reproduction. The implication of these hypotheses seems to be that natural selection favors maximizing reproduction to the extent allowable by environmental conditions.

In contrast, I proposed that natural selection for longer life (by reducing age-specific mortality) is the driving force in the evolution of life histories, with clutch size being minimized to the extent allowable by mortality, and that population size was limited, not regulated, by the availability of resources, predation, disease, or other sources of mortality or reduced reproductive success (Murray 1979, 1982, 1986, 1991a).

These fundamentally different perspectives of population dynamics may have implications for conservation biology, especially with regard to our understanding of the rates of decline and recovery. Consider a simple model of population growth (Murray 1979). In Figure 2 the birth and death rates in pristine natural conditions (i.e., before human interventions) are shown by the solid lines. Between the lower critical density (LCD) and the upper critical density (UCD) resources are sufficiently abundant that individuals have equal access to the resources that permit the expression of the maximum birth rate (given their evolved fecundity) and minimum death rate. Above the UCD the birth rate decreases

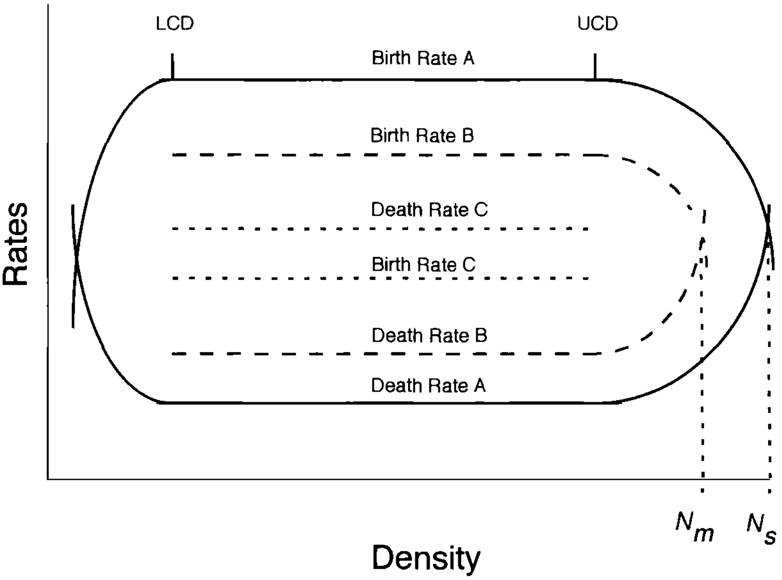

FIGURE 2. Relationship between a population's birth (*b*), death (*d*), and growth (*r*) rates, $r = \ln(1 + b—d)$, and its density. Birth and death rates A are natural rates unaffected by human intrusion. Birth and death rates B are those resulting from a moderate amount of anthropogenic increases in mortality. Birth and death rates C are those resulting from further anthropogenic increases in mortality, leading to eventual extinction. LCD = lower critical density, UCD = upper critical density, N_s = mean steady state size of population in natural conditions, and N_m = mean steady state size of population subjected to anthropogenic mortality rate B.

and death rate increases because of decreasing per capita availability of resources (e.g., food, space) or increasing levels of predation, disease, or other source of mortality. The population normally fluctuates in size around the mean steady-state size, N_s. Below the LCD the birth rate may decrease and the death rate may increase because the population is so small that individuals have difficulty in finding one another or in defending themselves from predators or other sources of mortality (e.g., Allee effects).

Second, consider that the exponential rate of change in numbers of a population (*r*) is a function of the difference between the birth (*b*) and death (*d*) rates (Murray 1997b),

$$e^r = \lambda = 1 + b - d, \qquad r = \ln(1 + b - d),$$

where *e* is the base of the natural logarithms and λ is the finite rate of change in population size. Between the LCD and UCD in Figure 2, $r_{max} = \ln(1 + b_{max} - d_{min})$, which corresponds to the population's natural biotic potential.

In Figure 2 the long dashed lines show the effects on birth and death rates of a moderate increase in mortality (the birth rate decreases with increasing mortality because of a changing age structure; Murray 1979). With moderate mortality, the mean steady-state population size, N_m, is smaller than N_s. With greater anthropogenic mortality, the death rate increases and the birth rate decreases further. If the death rate exceeds the birth rate ($r < 0$), as shown by the short dashed lines in Figure 2, the population declines toward extinction (i.e., size and density decrease).

The rate at which a population recovers from decline (that is, increases in numbers, *r*) is a function of how well humans have managed to clean up the environment and to reduce predation, disease, and other sources of anthropogenic mortality. The maximum rate of increase is r_{max}, that is the population's theoretical biotic potential, unless management has also reduced the natural causes of mortality.

Indeed, anthropogenic activity may affect all species, reducing predator populations as well as prey. A decline in predators could result in increasing r_{max} of the prey and greater N_s, but the latter only if predation limited population size. I suspect that populations of most passerine species, if not most species of birds, are limited by territorial behavior (Murray 1979, 1982). The elimination of predators in territorial species could result in a greater r_{max} but not in a greater population size, N_s. The beauty of the model in Figure 2 is that one can plot the consequences of multiple causes of mortality, as shown in greater detail in Murray (1986).

TABLE 2. LIFE HISTORY PARAMETERS OF GROWING (r_{max} = 0.05) LONG-LIVED (A) AND SHORT-LIVED (B) POPULATIONS

Parameter	Population A	Population B
Survival during first year ($s_{x=1}$)[a]	0.40	0.15
Survival after first year ($s_{x>1}$)[a]	0.80	0.50
Age class[a] of first breeding (α)	4	2
Maximum age class[a] (ω)	27	10
Mean fecundity of breeders (m_x)[a]	1.1420	3.8685
Generation time (T)	7.8861	2.9824
Birth rate (b)	0.4058	0.8266
Death rate (d)	0.3545	0.7754
r_{max}	0.05	0.05

[a] x = age class = age + 1 (Murray 1997b).

We can examine the dynamics of population change further by comparing, quantitatively, the effects on a population's growth rate (r) of increasing amounts of pollution, predation, or disease in populations with different life histories. For illustration (Table 2), I have created for comparison a long-lived, low-fecundity population, A, and a short-lived, high-fecundity population, B. I have assumed for each an r_{max} of 0.05 in pristine environments. With increasing intensity of mortality, the death rate increases, the birth rate decreases, and, thus, r decreases (Fig. 3). What is striking in this example is the much greater risk of extinction of the short-lived, high-fecundity population exposed to the same intensity of anthropogenic mortality as the long-lived, low-fecundity population. This result seems counterintuitive.

Indeed, Freed (1999) has pointed out that species of endangered Hawaiian honeycreepers (Kaua‘i Creeper [*Oreomystis bairdi*] and Kaua‘i ‘Ākepa [*Loxops caeruleirostris*]) have small clutch sizes and tend to be single brooded, compared with the more abundant species (Kaua‘i ‘Amakihi [*Hemignathus kauaiensis*], ‘Apapane [*Himatione sanguinea*], and I‘iw‘i) living in ‘ōhi‘a-koa forest on Kaua‘i. These data and the result shown in Figure 3 indicate to me that, for some reason, low-fecundity species must have a smaller r_{max} than high-fecundity species. Low-fecundity species are at greater risk because of a naturally low r_{max} rather than a low fecundity per se. We should consider how differences in r_{max} could evolve.

First, if age-specific survival and longevity (i.e., s_x and l_x, respectively) reflect density-dependent responses to the evolution of clutch size and, therefore, fecundity (i.e., m_x = (mean clutch size × mean number of clutches)/2), as implied by Lack (1947, 1948, 1954, 1966) and Cody (1966), or if clutch size, survival, and longevity are optimized, as suggested by Williams (1966) and Charnov and Krebs (1974), the situation described in Table 2 and Figure 3 is possible. We should expect to find some long-lived, low-fecundity species with an r_{max} that is equal to or

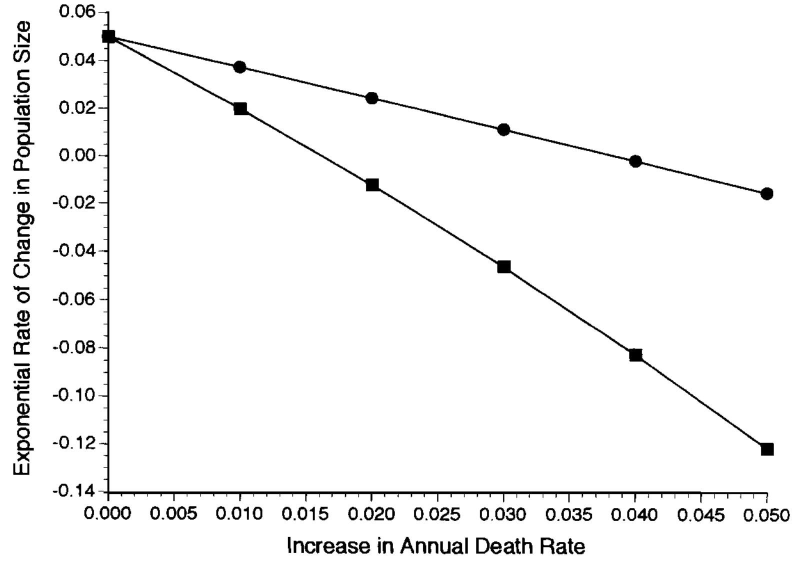

FIGURE 3. A comparison of the effect of r_{max} (i.e., between the LCD and UCD in Figure 2) of increases in the death rate from increasing anthropogenic causes of mortality in a long-lived, low-fecundity population A (circles) and short-lived, high-fecundity population B (squares). The data for each population when r_{max} = 0.05 are given in Table 2.

TABLE 3. LIFE HISTORY PARAMETERS OF LONG-LIVED (C) AND SHORT-LIVED (D) STEADY-STATE ($r = 0$) POPULATIONS

Parameter	Population C	Population D
Survival during first year ($s_{x=1}$)[a]	0.310	0.126
Survival after first year ($s_{x>1}$)[a]	0.710	0.476
Age class[a] of first breeding (α)	4	2
Maximum age class[a] (ω)	27	10
Mean fecundity of breeders (m_x)[a]	1.4621	4.164
Generation time (T)	6.4418	2.8971
Birth rate (b)	0.4834	0.8063
Death rate (d)	0.4834	0.8063
r_{max}	0.0000	0.0000

[a] x = age class = age + 1 (Murray 1997b).

even greater than the r_{max} of some short-lived, high-fecundity species. In the long-lived population in our example, the mean annual m_x is 1.1420 of breeders (some females should be laying three or more eggs [i.e., mean = 2 × 1.1420] per year) and is sufficient to maintain r_{max} at 0.05 with its survivorship schedule. In the short-lived population, the mean annual m_x is 3.8695 of breeders (some females should be laying eight or more [i.e., mean = 2 × 3.8695] eggs per year) and is sufficient to maintain r_{max} at 0.05 with its survivorship schedule.

According to the theories of Lack, Cody, Williams, and Charnov and Krebs, there is no apparent reason for r_{max} to be smaller in a low-fecundity, long-lived population. For example, suppose a mutation occurs that allows the long-lived females in population A (Table 1) to lay on average an additional egg per year ($m_x = (2.284 + 1)/2 = 1.642$). Suppose further that the larger fecundity reduces survival during the first year from 0.40 to 0.35 and survival of females of breeding age from 0.80 to 0.75. Under these conditions, $r_{max} = 0.0576$. Thus, the benefit of an increase in fecundity exceeds the cost of decreasing survival, resulting in an increase in r_{max}. If the new, larger fecundity should evolve because it is "optimal," we should expect to find at least some low-fecundity species with a high r_{max} and, therefore, with a lower risk of extinction than some high-fecundity species.

On the other hand, according to my theory, selection acts on clutch size when the population is fluctuating around the population's mean size, N_s, that is, when $r = 0$ over evolutionary time (Murray 1999). If natural selection favors the genotype whose females lay as few eggs as are consistent with replacement because they have the highest probability of surviving to breed again, their young have the highest probability of surviving to breed, or both, as I have proposed (Murray 1979, 1991a, 1999), then we should expect r_{max} to be smaller in long-lived species than in short-lived species, according to the following argument.

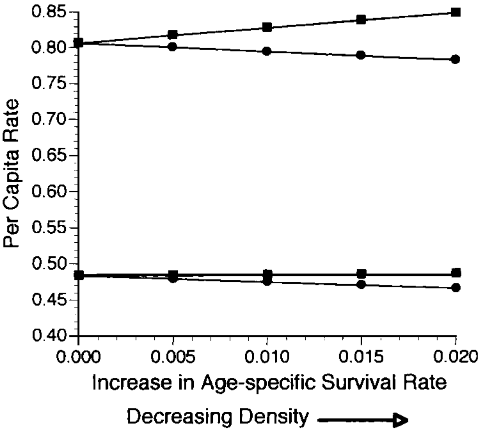

FIGURE 4. A comparison of the birth (squares) and death (circles) rates of long-lived population C (lower) and short-lived population D (upper) when their age-specific survival is increased above what is at N_s. Data for populations at N_s are in Table 3.

We can examine the demography of populations of different life histories by creating two new populations, a long-lived (C) and a short-lived (D) steady-state population (Table 3). According to the population dynamics model (Fig. 2), we should expect that the birth rate would be greater and the death rate smaller at population sizes less than N_s, compared with the birth and death rates at N_s. Assuming that age-specific fecundity within each population is the same at all densities, we can calculate the birth, death, and growth rates when age-specific survival is increased, simulating the effect of densities below N_s. For the same change in age-specific survival, the relative and absolute changes in birth and death rates are greater in the high-fecundity population than in the low-fecundity population, resulting in greater r (i.e., $\ln(1 + b - d)$) in the high-fecundity population (Fig. 4).

As far as I am aware, the notion that the clutch size reflects the fewest eggs that a female can lay, consistent with replacement, is the only explanation for the evolution of a smaller r_{max} in long-lived populations than in short-lived populations. Long-lived populations are not at greater risk of extinction than short-lived populations because of their lower fecundity per se but because of their smaller r_{max}. However intuitive it is that low-fecundity species should be at greater risk for extinction and have slower rates of recovery than high-fecundity species, current life-history theory does not explain it. On the other hand, the comparison of the demography of species at risk and not at risk comprises a small sample. Further comparisons would be desirable.

If selection results in a mean clutch size that just balances average mortality, as my theory asserts (Murray 1979, 1991a, 1999), then we should expect that island species, which usually have evolved in environments with little predation, disease, and other causes of mortality, should have greater mean life expectancy and lower fecundity than species exposed to greater natural mortality. Populations on islands, which have been assaulted by the introduction of disease (e.g., avian malaria), brood parasites (e.g., Glossy Cowbird [*Molothrus bonariensis*]), predators (e.g., rats, cats, and humans), as well as loss of habitat (e.g., to goats and humans), suffer disproportionately. Mainland populations, naturally subjected to higher mortality than island populations, have evolved larger clutch sizes and, thus, greater r_{max}. The mortality effects of a newly introduced predator should probably not be additive because the new predator would be expected to be competing with the already present predators, reducing the old predators' populations and their effect on the prey.

The conservation of endemic island populations will require preservation or restoration of suitable habitat and protection from predation and disease.

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