

NOTES AND COMMENTS

ON THE EVOLUTIONARY STABILITY OF DISPERSAL
TO SINK HABITATS

A recurring theme in the literature of population regulation is that surplus reproduction in high-quality "source" habitats is exported to low-quality "sink" habitats (Anderson 1970; MacArthur 1972; Lidicker 1975, 1985*a*, 1985*b*; Van Horne 1983). Two recent innovative papers by Pulliam (1988) and Pulliam and Danielson (1991) have shown that equilibrium densities in both kinds of habitats can be maintained by an evolutionarily stable strategy (ESS) of habitat selection. Yet the basic idea that populations exist indefinitely in habitats in which mortality exceeds recruitment seems counter to other evolutionary models that argue convincingly for habitat specialization (Rosenzweig 1974, 1981, 1985; Holt 1985). I show that emigration to sink habitats is likely to be an ESS only if there is reverse migration back to the source. Further, I propose that source-sink systems may have evolved not so much as evolutionarily stable dispersal strategies, but rather as necessary outcomes of other strategies that lead to the production of surplus recruits.

Pulliam partitioned habitat into compartments such that subpopulations living in source habitats produce a surplus of descendants ($\lambda > 1$), whereas subpopulations in sinks produce a deficit ($\lambda < 1$). The overall growth rate of all compartments is zero at equilibrium ($\lambda = 1$). The density in the sink is maintained by emigration from the source. The model assumes that source habitats are characterized by a relatively large number of high-quality sites at which individuals produce, during their lifetime, more offspring than that habitat can accommodate (Pulliam 1988; Pulliam and Danielson 1991). Because the number of breeding sites is also assumed to be limited, surplus recruits select those remaining sites that maximize their fitness, even if the offspring are unable to replace themselves. As long as there is surplus reproduction in the source, individuals following the habitat-selection rule, "never occupy a poorer breeding site when a better one is available" (Pulliam 1988, p. 657), will, at equilibrium, continue to colonize sink habitats.

In Pulliam's model, evolutionary stability is achieved through the assumptions of surplus reproduction and limited high-quality breeding sites. One interpretation of the model is that this EES has evolved from the rewards of colonization of sink habitats by individuals from surplus reproductive sources. Surplus reproduction,

however, is necessary for a variety of other evolutionary and ecological processes, including natural selection, sib competition, population growth, and the avoidance of extinction in variable or patchy environments. Dispersal to sink habitats may not have evolved as an ESS on its own account but rather as a necessary consequence of these and other processes. Evolutionary advantage for many kinds of dispersal may be unnecessary for its maintenance. Thus, it seems appropriate to ask, Under what conditions can emigration to reproductive sinks serve as a mechanism promoting surplus reproduction in source habitats?

Imagine a population occupying both source and sink habitats. Allow migration to occur between both types of habitat and assume that once an individual leaves a given habitat it is unable to return. Further assume that migration occurs before maturity and that it is instantaneous with no effect on reproduction or survival. For a stationary population, the eventual genetic contribution to the source subpopulation of one sexually reproducing female born in the source can be modeled as

$$\begin{aligned}
 W_{s0} &= (1 - m_{sk})V_{s0} + \frac{1}{2}m_{sk}V_{s0}m_{ks}V_{k0} + (1 - m_{ks})V_{k0}m_{ks}V_{k0} \sum_{r=2}^{\infty} (1/2)^r \\
 &= (1 - m_{sk})V_{s0} + \frac{1}{2}m_{sk}V_{s0}m_{ks}V_{k0} + \frac{1}{2}(1 - m_{ks})V_{k0}m_{ks}V_{k0},
 \end{aligned}
 \tag{1}$$

where V_{s0} is the reproductive value of an individual at birth in habitat s , m_{sk} is the probability of migration from habitat s to habitat k , $(1/2)^r$ corrects for the relatedness of future cohorts to the original female, and subscripts s and k stand for source and sink habitats, respectively. The term $m_{sk}V_{s0}$ is a measure of the number of offspring born in the source habitat that subsequently migrate to the sink; thus, $m_{ks}V_{s0}m_{ks}V_{k0}$ is the expected number of F_2 descendants born in the sink that eventually return to the source. Similarly, $(1 - m_{ks})V_{k0}$ is the number of F_2 offspring born in the sink that reproduce there, and $(1 - m_{ks})V_{k0}m_{ks}V_{k0}$ is the expected number of F_3 descendants born in the sink that eventually return to the source. The summation in the third term extends the contribution to all future (F_3 to F_{∞}) generations.

Setting equation (1) equal to unity at equilibrium and rearranging terms,

$$m_{sk}V_{s0} = \frac{2\{1 - [(1 - m_{sk})V_{s0} + \frac{1}{2}(1 - m_{ks})V_{k0}m_{ks}V_{k0}]\}}{m_{ks}V_{k0}}.
 \tag{2}$$

The solution to equation (2) gives the per capita surplus of descendants produced in the source habitat. This surplus can then be used to predict the relative abundance of individuals living in both source and sink habitats (Pulliam 1988).

Let us evaluate an extreme case in which dispersal to sink habitats is unidirectional. Dispersing individuals, and the genes they carry with them, are lost from the source population. Can such a strategy evolve from dispersal alone?

Consider two genotypes with equal access to resources in the source habitat. Assume that dispersal is the only selective force operating to create surplus reproduction. Genotype A, on the average, consistently produces a surplus of descen-

dants that disperse into sink habitats. Genotype B converts its resources into fewer descendants, each of which has a greater ability at obtaining sites in the source habitat than do those of genotype A. In order for habitat k to be a sink in the extreme sense, $m_{ks} = 0$. At equilibrium, a source female's fitness is $W_{s0} = (1 - m_{sk})V_{s0} = 1$. All surplus individuals produced by genotype A have zero fitness. If genotype B produces at least enough offspring of superior competitive ability to compensate for mortality within the source and if surplus reproduction by A entails decreased average survival of nondispersing offspring, B will replace A. B may be subsequently replaced by other genotypes that produce even fewer but more competitive descendants. From equation (2) we see that, at equilibrium, $1 - m_{sk}$ follows the negative exponential distribution, $1 - m_{sk} = (V_{s0})^{-1}$. $V_{s0} = 1$ at equilibrium; consequently, $m_{sk} = 0$, migration is nonexistent, and each individual female is, on the average, just replacing herself.

Dispersal to habitats that function as captive sinks does not represent an ESS in stable populations. This will not be the case for sinks in which descendants consistently reverse-migrate back to the source. Again setting equation (1) equal to unity at equilibrium, reverse migration means that $m_{ks} > 0$, and necessarily, $(1 - m_{sk}) < (V_{s0})^{-1}$. Consequently, genotypes that produce surplus offspring must have been favored by natural selection. Emigration from source habitats to dispersal sinks is likely to be an ESS only if there is some reverse migration back to the source. This analysis complements the genetic model of Bull et al. (1987), demonstrating that unidirectional migration between pairs of demes is not evolutionarily stable.

Pulliam's source-sink theory assumes that, up to some population threshold, all individuals in the source habitat can successfully occupy breeding sites. Beyond this threshold carrying capacity, the reproductive success of those individuals that do not occupy breeding sites is zero. Although this assumption is suitable for modeling "contest competitors" (Nicholson 1954), it is much less appropriate to "scramble competitors," for whom reproductive success may decline with increases in population density beyond carrying capacity (e.g., as when individual resource share decreases with rank, Łomnicki 1988). Density-dependent reduction in fitness has major implications for source-sink models of population regulation. Individuals in the source habitat are still able to reproduce, albeit with diminishing rewards, even though population density exceeds the habitat's carrying capacity. This means that the ESS of dispersal to sink habitats will be more difficult to achieve because the rewards of dispersal for any individual must exceed the nonzero reproductive value that could be gained by remaining in the source. The ESS is, similarly, more difficult to attain if migration entails reproductive and/or survival costs. Nevertheless, the basic criterion of nonzero migration of individuals from sink to source habitats is necessary for the source-sink model to represent an evolutionarily stable dispersal strategy.

Yet there is convincing evidence that many kinds of species occupy habitats where recruitment is unable to keep pace with mortality (Pulliam and Danielson 1991). There is similar evidence that the structure of ecological communities is often driven by recolonization processes (Ricklefs 1987; Roughgarden et al. 1987; Schroder 1987), and it is easy to conceive of scenarios (e.g., the influence of wind

and currents on the dispersal of seeds, spores, and larvae) in which propagules consistently arrive in sink habitats with zero probabilities of subsequent reproduction. This note demonstrates that the surplus of individuals available to colonize such habitats is unlikely to be produced solely from ESSs of dispersal to sinks. Although reverse migration from dispersal sinks can enhance surplus reproduction in source habitats, such surpluses are more likely the result of other life history and competitive strategies that favor the overproduction of offspring.

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