

NOTES AND COMMENTS

HOW DOES IMMIGRATION INFLUENCE LOCAL ADAPTATION? A REEXAMINATION OF A FAMILIAR PARADIGM

ROBERT D. HOLT^{1,*} AND RICHARD GOMULKIEWICZ^{2,†}

¹Department of Systematics and Ecology and Museum of Natural History, Dyche Hall, University of Kansas, Lawrence, Kansas 66045; ²Department of Systematics and Ecology, Haworth Hall, University of Kansas, Lawrence, Kansas 66045

Submitted January 26, 1996; Revised June 14, 1996; Accepted June 14, 1996

All species are distributed in space, but within limits. What determines these limits through evolutionary time is an important issue that is receiving increased attention (Hoffman and Blows 1994). For instance, paleobiologists have suggested that species' climatic range limits often reveal long-term stasis (Huntley et al. 1989), which presumably reflects stasis in basic ecological traits (e.g., physiological tolerance to climatic extremes).

Stasis in species' borders provides a particularly compelling category of "niche conservatism"—the observation that phylogenetic lineages often seem to retain much the same ecological niche over substantial spans of evolutionary history (Holt and Gaines 1992; Ricklefs and Latham 1992; Holt 1996). There are three basic classes of explanations for niche conservatism, particularly at species borders: an absence of appropriate genetic variation (Bradshaw 1991; Bradshaw and McNeilly 1991); conservative selection, either within populations (Holt and Gaines 1992; Holt 1996) or among populations (Gomulkiewicz and Holt 1995), preventing evolutionary change in the niche; and gene flow swamping local selection (Mayr 1963).

The third class of explanations may apply even if gene flow is not great enough to prevent local differentiation in response to spatially varying selection in much of the interior of a species' range (Endler 1977). Antonovics (1976) observed that peripheral populations may exist at densities considerably lower than more central populations. Rates of immigration that are low in absolute terms but high relative to the local population's abundance may suffice to swamp out local selec-

* E-mail: predator@kuhub.vc.ukans.edu.

† Present address: Department of Genetics and Cell Biology and Department of Pure and Applied Mathematics, Washington State University, Pullman, Washington 99164; E-mail: gomulki@wsu.edu.

tion. This points out the importance of placing analyses of evolutionary dynamics in an appropriate demographic context. In this note, we will argue that a clear understanding of population dynamics is, in fact, essential to understanding the influence of immigration on niche conservatism at species' borders or, for that matter, on niche conservatism in any species with "sink" populations maintained outside its current niche by immigration.

The standard interpretation of adaptive evolution in a local population coupled by dispersal to other populations emphasizes the relative strength of opposing forces: natural selection, favoring locally fitter genes, and gene flow, reducing the frequency of locally favored genes. For a wide range of models (see below for a typical example), one can compare the impacts of these two forces using a rule of thumb: for a given selective advantage of a locally favored allele, there is some rate of gene flow below which that allele will spread when rare. Hence, the greatest scope for local adaptation should occur at low to zero rates of gene flow.

Now suppose the local population is a "sink" population, that is, one that would go extinct deterministically without recurrent immigration (Shmida and Ellner 1984; Pulliam 1988; Holt 1993). If we apply the prior rule of thumb to such a population, it leads to an absurd conclusion. While zero immigration provides the widest scope for local adaptation, a sink population without immigration goes extinct. And there is, of course, little scope for evolution in extinct populations.

We will argue that it is sensible to change the frame of reference for analyzing adaptive evolution in sink populations. Population genetic models are typically cast in terms of gene frequency and relative fitness. To account for the demographic consequences of immigration, however, one also needs to account for changes in population size, in effect examining dynamics in gene numbers rather than in gene frequencies and using absolute rather than relative fitness (see also Ginzburg 1983; Svirezhev and Passekov 1990). In this note, we show that this change in the frame of reference leads to a fresh perspective on the manner in which gene flow hampers local selection, particularly in sink populations.

First, we examine a simple one-locus haploid model incorporating population dynamics, local selection, and gene flow. We then discuss the consequences of incorporating density dependence and briefly outline the salient conclusions of a comparable diploid model.

A MODEL INCORPORATING GENE FLOW AND LOCAL SELECTION

Consider the following "island" model for niche evolution in a sink population with discrete generations and one-locus haploid (or clonal) genetic variation. We will assume in particular that evolution in the sink has no back effect on the source population; this is the black-hole sink scenario discussed elsewhere (Holt and Gaines 1992). There are two genotypes, A_1 and A_2 . Let W_i be the absolute fitness of genotype A_i on the island. Assume genotype A_1 has a higher fitness in the local environment (i.e., $W_1 > W_2$). Let p be the local frequency of A_1 and $\bar{W} = pW_1 + (1 - p)W_2$ be the mean fitness of the local population. Each generation, migration occurs after selection; we census the population immediately after migration. First, assume one-way migration into the island occurs at a per-

generation rate, m , which is expressed as the percentage of the censused population composed of migrants. For simplicity, we assume all immigrants are of the less fit genotype A_2 . Further, we assume fitnesses are density independent (we relax this assumption later). This ecological assumption about the absence of density dependence in a sink habitat describes some natural populations. For instance, Keddy (1981, 1982) describes an example of a sink population of a sand-dune annual plant, *Cakile edentula*, maintained by immigration, in which birth and death rates were density independent in the sink habitat. With these assumptions,

$$p' = (1 - m) \left(\frac{W_1}{\bar{W}} \right) p \quad (1)$$

describes how gene frequency changes each generation because of both selection (the right-bracketed term) and gene flow (the left-bracketed term) (see, e.g., Nagylaki 1977).

When A_1 is rare ($p \approx 0$), $\bar{W} \approx W_2$. After substituting this term into equation (1), the condition for A_1 to increase in frequency when rare becomes

$$\frac{W_1}{W_2} > \frac{1}{1 - m} > 1. \quad (2)$$

Condition (2) states that whether local adaptation occurs depends on both the migration rate and the *relative* fitnesses of the two genotypes. This indicates a rule of thumb for adaptive evolution on the island: for given fitnesses (W_1, W_2), there is a rate of migration, m , below which local adaptation (\equiv spread of A_1) will occur. Note that the maximal scope for local adaptation occurs as $m \rightarrow 0$.

We now reanalyze this same island model scenario but track gene number rather than gene frequency. Let N_1 be the number of genotype A_1 and $N = N_1 + N_2$ denote total population size. Consider first the dynamics of a population fixed for the less fit, immigrant genotype, so that $N = N_2$. Because we assume that the island contains a sink population that cannot persist without immigration, the absolute fitness of genotype A_1 is < 1 ($W_2 < 1$). If a constant number I of A_2 individuals immigrate to the island each generation, then total population size changes in accord with

$$N' = NW_2 + I.$$

The sink population equilibrates at density

$$\hat{N} = \frac{I}{1 - W_2} \equiv \hat{N}_2. \quad (3)$$

A large sink population will be maintained at equilibrium if there is a high immigration rate and a moderate rate of decline in the sink (i.e., W_2 near 1) (Holt 1993).

Now consider what would happen if a number N_1 of the other, locally more fit genotype were introduced. The frequency of A_1 is $p = N_1/(N_1 + N_2)$. Because we have assumed that A_1 is not present in the immigrant stream, its dynamics are described simply by

dependent viability of genotype A_i up to immigration, where $N = N_1 + N_2$ is the census number of zygotes. If all selection and density regulation occurs before the arrival of immigrants, then the dynamics can be described by equations (4) and (6), with W_i replaced by $W_i(N)$:

$$N' = N\bar{W}(N) + I \quad (8)$$

and

$$p' = \left(\frac{N}{N'}\right) W_1(N)p, \quad (9)$$

where $\bar{W}(N) = pW_1(N) + (1 - p)W_2(N)$.

Because the habitat is assumed to be a sink for the immigrant genotype, $W_2(N) < 1$ for all $N \geq 0$. This should preclude phenomena such as chaotic dynamics (Holt 1983). Assume as before that the sink population is near fixation for A_2 and is also near its associated demographic equilibrium. That is, assume $p \approx 0$ and $N \approx N' \approx \hat{N}_2$, where \hat{N}_2 is the equilibrium density in the absence of A_1 (i.e., \hat{N}_2 is a positive solution of $N = [NW_2(N) + I]$; see eq. [8]). Then, by equation (9),

$$p' \approx W_1(\hat{N}_2)p.$$

Thus, as before (cf. eq. [7]), A_1 will increase when rare if and only if its absolute fitness, $W_1(\hat{N}_2)$, exceeds 1. That is, absolute rather than relative fitness governs the spread of a rare, locally favored genotype in a sink population, density regulated or not. This criterion is independent of any direct effect of the rate of immigration on the frequency recursion. If increasing the immigration rate I increases \hat{N}_2 , absolute fitnesses will be depressed. Qualitatively, an increase in I that depresses absolute fitness changes a fitness array like that of figure 1A to one like that of figure 1B. In this way, immigration may indeed hamper local adaptation but via an ecological effect resulting from local density dependence. (Similar conclusions result if density regulation and selection occur after immigration; R. Gomulkiewicz and R. D. Holt, unpublished results.)

To the extent that increasing density tends to depress individual fitness, this shows that the density-independent analysis in the previous section provides a "best-case scenario" for initial increase of a rare locally favored genotype, in the sense that the requirements for A_1 to invade are more stringent with density dependence in the sink than without (see also Gomulkiewicz and Holt 1995). If the equilibrium sink density in the absence of A_1 , \hat{N}_2 , is not large, density effects should be relatively unimportant in determining the initial spread or loss of a locally favored allele, and the density-independent model of the previous section should be an adequate representation of initial evolution in the sink.

These results for a density-regulated sink population show that the absolute fitness criterion for increase is not an artifact of the potential for unbounded population growth in the density-independent model. Rather, the absolute fitness criterion arises from the fundamental requirement that a population, density regulated or not, must persist to adapt to a local environment.

Finally, we have analyzed the conditions for spread of a rare, locally favored

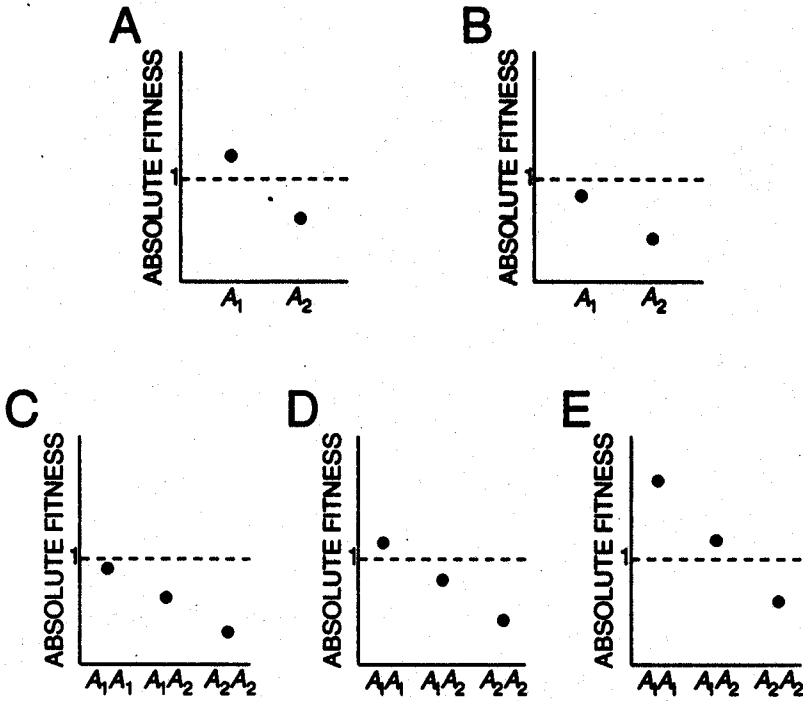


FIG. 1.—Sets of absolute fitnesses in a sink population, determined by genotypes at a haploid or diploid locus with alleles A_1 and A_2 that lead to qualitatively different population and evolutionary dynamics assuming immigrants are monomorphic for allele A_2 . *A, B*, Fitnesses determined by a haploid locus such that $W_2 < 1$. Relative fitnesses are identical for the two examples shown: $W_1/W_2 = 2$. As discussed in the text, A_1 will increase when rare, as in *A*, whereas in *B*, it does not. One effect of density dependence may be to alter fitnesses, changing an array like that in *A* to one resembling that in *B*. *C–E*, Fitnesses determined by a diploid locus (for details, see Holt and Gomulkiewicz, in press; R. Gomulkiewicz and R. D. Holt, unpublished data). The absolute fitness of genotype A_iA_j is denoted by W_{ij} . Immigrants arrive at a rate I per generation and are assumed to be homozygous for allele A_2 , with local absolute fitness $W_{22} < 1$. The relative fitnesses are identical for the three examples shown: $W_{11}/W_{12} = 1.5$ and $W_{22}/W_{12} = 0.5$. *C*, All absolute fitnesses are < 1 ; A_1 will always be excluded. *E*, Heterozygote absolute fitness is > 1 , allowing the locally fitter allele to increase in frequency when rare. *D*, Heterozygote absolute fitness is < 1 so A_1 will not invade when rare; invasion requires that A_1 be sufficiently common. In the absence of density dependence, the threshold initial frequency for allele A_1 , below which it is excluded and above which it increases, is independent of the rate of immigration (Holt and Gomulkiewicz, in press).

allele at a diploid locus in an island sink population (for more details, see Holt and Gomulkiewicz, in press; R. Gomulkiewicz and R. D. Holt, unpublished data). As in the haploid model, the criterion for initial increase of a rare allele in a population maintained by immigration depends on absolute rather than relative fitness. In this case, the relevant absolute fitness is that of heterozygotes that carry the favored allele. If the allele is sufficiently rare and p is its frequency, the initial dynamics of the allele are described approximately by

$$p' \approx W_{\text{het}}P, \quad (10)$$

where W_{het} is the absolute fitness (possibly density dependent) of heterozygous individuals that carry the allele. The criterion for initial spread in the diploid case is again independent of any direct influence of the immigration rate of the maladapted genotype, although immigration may have an indirect influence via an ecological effect as described earlier if fitness is density dependent (R. Gomul-kiewicz and R. D. Holt, unpublished data). Figure 1C–E encapsulates the main results of the diploid model.

DISCUSSION

Our analyses lead to three main conclusions. First, a hidden assumption is often made in traditional population genetics models (e.g., eq. [1]) and thus in the evolutionary inferences drawn from such models—namely, that the gene flow parameter, m , is fixed. However, models such as ours that pay attention to the demographic consequences of both migration and selection show that m may actually be a dependent variable and in particular can indirectly depend on local fitnesses. When immigration can affect population size, for populations at or near demographic equilibrium, there is a necessary relationship between the gene flow parameter and local fitness. Indeed, it is misleading to refer to a gene flow “parameter” at all, since its magnitude varies with population size.

Second, our analyses of one-locus models show that an absolute rather than relative fitness criterion governs the deterministic spread of a locally favored allele in a sink population. This effect was observed in a sketchy form previously (Holt and Gaines 1992). This criterion in effect arises from the requirement that a population must persist to adapt.

Third, in the absence of local density dependence, the rate of immigration, I , is causally irrelevant to the initial spread of a locally favored allele (given $I > 0$). By comparison, standard population genetic models based on gene frequencies seem to reflect two distinct evolutionary “forces”: gene flow and natural selection. However, our analyses of one-locus models using a different frame of reference, namely, gene numbers, show that the availability of variants with absolute fitnesses >1 is the sine qua non of adaptive evolution in sinks. In this shifted frame of reference, the “force” of gene flow disappears—somewhat as the “Coriolis force” perceived by observers on the Earth’s surface disappears when using a frame of reference outside.

The existence of an absolute fitness criterion for determining the evolutionary fate of an allele in a sink habitat has two potentially important implications. First, the constraining influence of migration on local adaptation in a sink environment arises because immigrants determine the baseline for evolutionary change. That is, the difference between the fitness of the immigrant type (i.e., $W_2 < 1$) and unity defines an “adaptive threshold.” The change in absolute fitness produced by a given genetic mutation must exceed this adaptive threshold if the mutation is to spread because of selection. The “worse” the sink habitat is (i.e., the lower the fitness of the immigrant type), the larger the adaptive threshold will be, and

the larger the mutational effect permitting spread of a locally favored allele must be. Density dependence in the sink can aggravate this effect.

This observation suggests that mutants of small effect on individual fitness typically cannot invade a sink habitat. Only mutants of sufficiently large positive effect on absolute fitness can increase when rare. Part of the conventional wisdom of evolutionary biology has long been that adaptive evolution largely rests on the accumulation of genetic changes, each of small effect. The above models clearly highlight one circumstance, namely, sink populations maintained by immigration, where this mode of adaptive evolution is precluded.

The second implication is that local adaptation (fitness maximization) only occurs if mutants arise that can permit the population to persist without immigration. In other words, adaptive evolution in a sink habitat is essentially synonymous with niche evolution. If mutants of large effect on fitness are rare, one automatically expects "niche conservatism" in a spatially heterogeneous environment, particularly if initial fitness in the sink environment is very low.

Making fitnesses density dependent provides one means by which the rate of immigration can directly influence the chances for local adaptation, via its effect on absolute fitness. All else being equal, with density dependence, higher rates of immigration will usually lead to higher local densities and lower fitnesses (Holt 1983). When an allele is rare, it will still be true that equation (10) approximately describes the initial dynamics of a diploid locus, but the heterozygote fitness (and hence the scope for adaptive evolution) may be depressed below unity by density-dependent reductions in fitness. Because of density dependence, some locally favored alleles may be able to invade at low immigration rates but be excluded at high rates. This suggests that immigration may indeed in some circumstances hamper local adaptation, although the actual mechanism is ecological rather than genetic. Moreover, a necessary criterion for an allele to increase when rare is still that its absolute fitness at low densities must exceed 1, regardless of density dependence.

Because a locally favored allele can increase when rare, a polymorphic equilibrium will be attained with the population equilibrating at a total density greater than that which would be permitted by immigration alone if such an allele were excluded (Holt and Gomulkiewicz, in press). This population is one that could persist deterministically were immigration cut off. Such a polymorphic population, by definition, lies within its species' niche. Indeed, in a persistent population increased immigration may depress local abundance; the existence and magnitude of this effect depends on ecological and genetic details (Holt 1983).

There are, of course, limitations in the models that we have treated here. It is useful to briefly consider some changes that might conceivably alter our conclusions.

We have assumed a unidirectional flow of immigrants from source to sink habitats. An important direction for future work will be examining adaptive evolution given reciprocal dispersal between source and sink populations. In effect, this would generalize the results of other studies (Holt and Gaines 1992; Kawecki 1995; Holt 1996). In our models, immigration rates and fitness parameters are assumed to be temporally constant. Without density dependence, variable immi-

gration rates appear not to introduce any novel influences on conditions for initial increase of a locally favored allele (R. Gomulkiewicz and R. D. Holt, unpublished data). With variable fitnesses, a geometric mean fitness criterion arises; temporal variation in fitness could hamper local adaptation. With density dependence, analyzing the consequences of temporal variation in immigration or fitness parameters for the evolution of local adaptation is a challenging task.

It is also possible that unforeseen effects of immigration on niche evolution could arise because of genetic linkage and epistasis or from sampling effects associated with finite population size. Explicit multilocus genetic models and models incorporating demographic stochasticity and genetic drift will be needed to assess the potential impact of these factors. (Straightforward extensions of standard quantitative genetic models to evolution in a sink population should be viewed skeptically, however, because one cannot assume that an admixture of residents and immigrants leads to a normal distribution.)

Finally, increased immigration may sometimes facilitate adaptive evolution in a sink, contrary to conventional wisdom. This is because local population size N in a sink increases with I , increasing the absolute rate of appearance of novel, potentially beneficial mutations. Moreover, immigration samples from existing variation in the source population; an increase in I provides a larger sample from source variation, thereby promoting the rate of arrival of locally favored immigrants. Evaluating the importance of these effects requires the development of models that explicitly incorporate mutational input and source population sampling.

It is important to keep in mind that our results do not undermine the standard population genetic conclusions regarding the interplay between gene flow and selection, particularly with respect to the adaptation of populations to localized environments in the interior of their species' range, that is, to environments with conditions already within their species' niche. However, for peripheral populations inhabiting environments currently outside their species' niche (i.e., sink populations), explanations of constraints on local adaptation that are based solely on gene flow hampering local selection should be rethought in light of our results, which explicitly account for population dynamics.

ACKNOWLEDGMENTS

We thank B. Walsh and two anonymous reviewers for their comments on a previous version of this note. This work was supported in part by National Science Foundation grant DEB-9528602.

LITERATURE CITED

- Antonovics, J. 1976. The nature of limits to natural selection. *Annals of the Missouri Botanical Garden* 63:224-247.
- Bradshaw, A. D. 1991. The Croonian Lecture 1991: genostasis and the limits to evolution. *Philosophical Transactions of the Royal Society of London B, Biological Sciences* 333:289-305.
- Bradshaw, A. D., and T. McNeilly. 1991. Evolutionary response to global climate change. *Annals of Botany* 67(Suppl. 1):5-14.

- Endler, J. A. 1977. Geographic variation, speciation, and clines. Princeton University Press, Princeton, N.J.
- Ginzburg, L. R. 1983. Theory of natural selection and population growth. Benjamin/Cummings, Menlo Park, Calif.
- Gomulkiewicz, R., and R. D. Holt. 1995. When does evolution by natural selection prevent extinction? *Evolution* 49:201-207.
- Hoffman, A. A., and M. W. Blows. 1994. Species borders: ecological and evolutionary perspectives. *Trends in Ecology & Evolution* 9:223-227.
- Holt, R. D. 1983. Immigration and the dynamics of peripheral populations. Pages 680-694 in A. G. J. Rhodin and K. Miyata, eds. *Advances in herpetology and evolutionary biology*. Museum of Comparative Zoology, Harvard University Press, Cambridge, Mass.
- . 1993. Ecology at the mesoscale: the influence of regional processes on local communities. Pages 77-88 in R. Ricklefs and D. Schluter, eds. *Species diversity in ecological communities: historical and geographical perspectives*. University of Chicago Press, Chicago.
- . 1996. Demographic constraints in evolution: towards unifying the evolutionary theories of senescence and niche conservatism. *Evolutionary Ecology* 10:1-11.
- Holt, R. D., and M. S. Gaines. 1992. Analysis of adaptation in heterogeneous landscapes: implications for the evolution of fundamental niches. *Evolutionary Ecology* 6:433-447.
- Holt, R. D., and R. Gomulkiewicz. In press. The evolution of species' niches: a population dynamic perspective. Pages 25-50 in H. G. Othmer, F. R. Adler, M. A. Lewis, and J. C. Dalton, eds. *Case studies in mathematical modeling: ecology, physiology, and cell biology*. Prentice Hall, New York.
- Huntley, B., P. J. Bartlein, and I. C. Prentice. 1989. Climatic control of the distribution and abundance of beech (*Fagus L.*) in Europe and North America. *Journal of Biogeography* 16:551-560.
- Kawecki, T. J. 1995. Demography of source-sink populations and the evolution of ecological niches. *Evolutionary Ecology* 9:38-44.
- Keddy, P. A. 1981. Experimental demography of the sand-dune annual, *Cakile edentula*, growing along an environmental gradient in Nova Scotia. *Journal of Ecology* 69:615-630.
- . 1982. Population ecology on an environmental gradient: *Cakile edentula* on a sand dune. *Oecologia (Berlin)* 52:345-355.
- Mayr, E. 1963. *Animal species and evolution*. Harvard University Press, Cambridge, Mass.
- Nagylaki, T. 1977. *Selection in one- and two-locus systems*. Springer, Berlin.
- Pulliam, H. R. 1988. Sources, sinks, and population regulation. *American Naturalist* 132:652-661.
- Ricklefs, R. E., and R. E. Latham. 1992. Intercontinental correlation of geographical ranges suggests stasis in ecological traits of relict genera of temperate perennial herbs. *American Naturalist* 139:1305-1321.
- Shmida, A., and S. Ellner. 1984. Coexistence of plant species with similar niches. *Vegetatio* 58:29-55.
- Svirezhev, Y. M., and V. P. Passekov. 1990. *Fundamentals of mathematical evolutionary genetics*. Kluwer Academic, Dordrecht.

Associate Editor: J. Bruce Walsh