Allee Effects in Metapopulation Dynamics

Priyanga Amarasekare*

Department of Ecology and Evolutionary Biology, University of
California, Irvine, California 92697-2525

Nearly all metapopulation theory is rooted in the patch
occupancy framework of Levins (1969, 1970). The Levins
model is a powerful metaphor for population dynamics
in patchy environments (Gilpin and Hanski 1991; Hanski
and Gilpin 1996; Kareiva and Wennergren 1995). It also
provides a conceptual framework for understanding the
effect of habitat fragmentation on population and com-
munity persistence (Caughley 1994; Harrison 1994).

In the Levins framework, per capita metapopulation
growth rate increases as the number of occupied patches
decreases, causing metapopulations to increase when
rare. Little or no attention has been paid to the possibil-
ity that the per capita growth rate may decrease at low
habitat occupancy, causing metapopulations to go extinct
when rare.

Single populations go extinct when rare due to Allee
effects (Allee 1931): scarcity in reproductive opportuni-
ties that cause negative growth rates below a critical den-
sity threshold (Dennis 1989; Lewis and Kareiva 1993;
Kunin and Iwasa 1996). Here I investigate how Allee ef-
fects influence metapopulation dynamics. I use the Lev-
ins model as a point of departure.

The Levins Model: Metapopulations
Increase When Rare

The Levins model can be written in the nonstandard
form

$$\frac{dp}{dt} = (m - e)p\left(1 - \frac{p}{1 - \frac{e}{m}}\right), \qquad (1)$$

* E-mail: pamarase@uci.edu.

where p is the fraction of habitats occupied by the species
in question, m is the colonization rate of empty patches,
and e is the extinction rate of occupied patches. The
nontrivial equilibrium $p^* = 1 - (e/m)$ is globally stable
as long as $m > e$.

The Levins model is directly analogous to the logistic
model $dN/dt = rN[1 - (N/K)]$ (Gilpin and Hanski
1991; Caughley 1994). For example, $m - e$ is equivalent
to the intrinsic rate of increase r, $(m - e)\{1 - p/[1 -
(e/m)]\}$ to the per capita growth rate $r[1 - (N/K)]$, and
$1 - (e/m)$ to K, the carrying capacity of the single popu-
lation.

As in the logistic, the negative density dependence in
the per capita growth rate ensures that the metapopula-
tion increases when rare as long as the intrinsic growth
rate is positive.

An important assumption in both models is that N
and p are large so that they can be considered continuous
variables. In the Levins model this translates to a large
number of habitat patches occupied by many local popu-
lations (Hanski et al. 1996). However, most real meta-
populations that persist via extinction-colonization dy-
namics (Harrison 1991) are found in small to moderate
networks of patches (Sjogren 1991; Hanski 1996; Thomas
and Hanski 1996). More often than not, the number of
occupied patches in such networks is quite small (Pelto-
nen and Hanski 1991; Thomas 1994, Hanski et al.
1995a).

The analogy between logistic and Levins models pro-
vides a simple way to explore effects of small meta-
population size.

The logistic model with an Allee effect depicts a single
population that goes extinct when rare. For example,

$$\frac{dN}{dt} = rN\left(1 - \frac{N}{K}\right)\left(\frac{N}{K} - \frac{A}{K}\right), \qquad (2)$$

where A ($0 < A < K$) is the threshold population size
below which $dN/dt < 0$ due to Allee effects (Dennis
1989; Lewis and Kareiva 1993).

Allee effects result from difficulty in encountering
mates at low densities (Lande 1987; Jennersten 1988;
Kunin 1993; Aizen and Feinsinger 1994). They typically
manifest as a disproportionate reduction in reproductive

success at small population sizes (Svane 1984; Robinson 1988; Lamont et al. 1993).

An Allee-like effect can occur at the metapopulation level. For example, colonization is the equivalent of reproduction in a metapopulation, and a metapopulation may suffer a disproportionate reduction in colonization success at small *p*. This may cause the per capita metapopulation growth rate to become negative below a threshold level of patch occupancy.

A Modified Levins Model: Metapopulations Go Extinct When Rare

An Allee effect can be introduced to the Levins model. For example,

$$\frac{dp}{dt} = (m - e)p\left(1 - \frac{p}{1 - \frac{e}{m}}\right)\left(\frac{p}{1 - \frac{e}{m}} - \frac{a}{1 - \frac{e}{m}}\right), \quad (3)$$

where $a(0 < a < 1 - [e/m])$ is the threshold fraction of occupied patches below which $(dp/dt) < 0$ and the metapopulation goes extinct.

The metapopulation now has multiple stable equilibria, 0 and $1 - (e/m)$. The nontrivial equilibrium $p^\star = 1 - (e/m)$ is stable if $m(1 - a) > e$. Unlike in the Levins model, $m > e$ is not sufficient to guarantee metapopulation persistence. The realized colonization rate is lower than *m* by a fraction *ma*. The quantity *ma* represents the reduction in the probability of successful colonization at low *p*.

Dispersal costs as well as difficulties in establishment may contribute to a low realized colonization rate at small *p*. Since only a few patches are occupied, the number of propagules produced is likely to be small. These may not reach the empty patches if there is high dispersal mortality in transit. Dispersal incurs high costs for many species (Gaines and McLenaghan 1980; Loxdale et al. 1993; Small et al. 1993; Hammond 1995), particularly when the matrix that separates suitable habitat patches is uninhabitable. Conspecific attraction (Smith and Peacock 1990; Ray et al. 1991) and nonrandom migration (Hanski et al. 1994) may also reduce the number of individuals colonizing empty patches (Hanski 1996).

Difficulties during establishment may also lower the realized colonization rate. If the number of colonists arriving in a patch is small, regular Allee effects may prevent them from increasing above the extinction threshold. This may be particularly important for animals in which reproduction occurs after migration (Hansson 1991; Hanski et al. 1994), for plants that rely on animal pollinators and seed dispersers (Jennersten 1988; Lamont

et al. 1993), and for species that exhibit high inbreeding depression (Lande et al. 1994). Even if there is no scarcity of reproductive opportunities at low densities, demographic stochasticity (May 1974; Shaffer 1987) may prevent successful establishment.

In sum, dispersal costs and difficulties in colonizing suitable habitat may lead to an extinction threshold at low *p*, creating an Allee-like effect. Such a metapopulation may not increase when rare, even when suitable habitat is abundant.

Biological Examples of Allee-Like Effects

Two lines of evidence suggest the operation of Allee-like effects in real metapopulations. The first comes from patch occupancy patterns. For example, *Daphnia* species that inhabit rock pools tend to be absent from islands with few rock pools (Hanski and Ranta 1983). British butterflies *Hesperia comma* and *Plebejus argus* are rarely found in regions with <10 patches (Thomas 1994; Thomas and Hanski 1996). *Melitaea cinixa*, a Finnish species, is often absent from small patch networks (Hanski et al. 1995*a*). A striking observation of all three species is a bimodal distribution of patch occupancy: most patch networks are either empty or fully (or nearly) occupied (Thomas 1994; Hanski et al. 1995*b*). This strongly suggests the presence of an extinction threshold at low habitat occupancy (Hanski and Gyllenberg 1993; Gyllenberg et al. 1996), consistent with an Allee-like effect at the metapopulation level.

A second line of evidence comes from species living in fragmented habitats. For example, habitat destruction has reduced the plant species *Banksia goodii* to a small number of populations (Lamont et al. 1993). About half the populations do not produce any seeds, mainly due to pollinator limitation. Given only a handful of viable populations separated by an inhospitable matrix, the potential for colonizing empty habitats is minimal. These attributes suggest that the system may be below the extinction threshold for a metapopulation. The same problem occurs in the Java hawk eagle (*Spizaetus bartelsi*), which is restricted to three forest reserves with few or no colonizing opportunities (Thiollay and Meyburg 1988). Similar effects due to habitat fragmentation, although not in an explicit metapopulation context, have been observed in plant-pollinator interactions as well (Jennersten 1988; Aizen and Feinsinger 1994).

Allee-Like Effects and Habitat Destruction

As the last set of examples suggests, Allee-like effects may be particularly important in species living in fragmented habitats. Extinction thresholds at low *p* may compound

the risks posed by habitat destruction. This can be illustrated by incorporating an Allee effect to the Levins model with habitat destruction.

The Levins model with habitat destruction (Kareiva and Wennergren 1995; Hanski et al. 1996) is

$$\frac{dp}{dt} = mp(h - p) - ep, \qquad (4)$$

where h is the proportion of suitable habitat remaining after habitat destruction ($h = 1$ with no destruction). The nontrivial equilibrium $p^* = h - (e/m)$ is globally stable as long as $e < mh$ (Hanski et al. 1996).

By analogy with the eradication threshold in epidemiology (Lawton et al. 1994; Nee 1994; Nee et al. 1996), the minimum proportion of habitat required for metapopulation persistence is $h - p^* = e/m$ (Hanski et al. 1996). So, even if $e < m,$ the metapopulation will go extinct if suitable habitat is destroyed beyond the threshold e/m (i.e., $h < e/m$). This idea has led to the general rule of thumb that metapopulation persistence is guaranteed as long as $h > e/m$ (Lawton et al. 1994; Nee 1994).

This approach ignores threshold effects due to small metapopulation size. Equation (4) predicts metapopulation persistence as long as $h > e/m$ (and $e < m$), regardless of how small the initial number of occupied patches is. However, if one incorporates an Allee effect to equation (4), one obtains

$$\frac{dp}{dt} = [mp(h - p) - ep]\left[\frac{m(p - a)}{mh - e}\right], \qquad (5)$$

with $0 < a < h - (e/m)$. The stable equilibria $p^* = 0$ and $h - (e/m)$ are now separated by the unstable equilibrium $a.$

The important point is that even if the proportion of suitable habitat h is above the eradication threshold, a metapopulation may still go extinct if the number of occupied patches is below the extinction threshold $a.$ For example, let $h > e/m$ and $a = e/m.$ Metapopulation persistence now requires $h > a + (e/m) = 2(e/m),$ twice the proportion of suitable habitat required under the Levins model.

Significance of Allee-Like Effects in Metapopulation Dynamics

Allee-like effects lead to metapopulation extinction thresholds at low habitat occupancy. Such thresholds are important for two reasons. First, they may prevent a metapopulation from increasing when rare even when suitable habitat is abundant. Second, they may compound metapopulation extinction risk due to habitat destruction.

Current metapopulation models do not adequately address these issues. For example, even models that explicitly consider small metapopulation size (Gurney and Nisbet 1978; Hanski et al. 1996) use the Levins framework and thus carry the implicit assumption that a metapopulation, when rare, always increases to carrying capacity. Hence, these models overestimate persistence times for metapopulations exhibiting Allee-like effects. Moreover, mean time to extinction is expressed as a combination of $p,$ which encapsulates the species' biology, and $H,$ the number of patches in the landscape (Hanski 1996). Therefore, this approach does not allow one to separate out effects due to small metapopulation size from those due to habitat destruction. This dependence is in fact implicit in most metapopulation models that investigate habitat destruction (Hanski et al. 1996).

The model I have presented allows one to quantify extinction risk due to small metapopulation size independent of habitat destruction. As the above analyses show, an Allee-like extinction threshold may prevent a metapopulation from increasing when rare even when habitat is plentiful and the expected growth rate is positive. It may cause a metapopulation of large size to unexpectedly go extinct if the occupied patch number falls below the threshold due to, say, a fire or a disease epidemic.

In previous metapopulation models, extinction thresholds are possible only in the presence of a rescue effect (Gyllenberg and Hanski 1992; Gyllenberg et al. 1996) and under the somewhat unrealistic assumption that colonization of empty patches remains low despite a high rate of dispersal among patches (Hanski and Gyllenberg 1993; Hanski et al. 1994). The model presented here suggests that metapopulation extinction thresholds may arise even in the absence of a rescue effect. This is particularly likely in species that experience high dispersal mortality or colonization difficulties due to Allee effects and demographic stochasticity.

The model predicts that Allee-like thresholds at low habitat occupancy may increase metapopulation extinction risk over and above that due to habitat destruction. Most conservation scenarios are likely to involve endangered species occupying only a small fraction of available habitat. These are the species most likely to experience high dispersal mortality or difficulties in colonizing suitable habitats due to Allee effects and demographic stochasticity. Predictions based solely on habitat availability may overestimate their ability to persist in the long term.

Many studies of metapopulation processes have focused on extinction events. The simple model presented here suggests that the details of colonization may be just as important, particularly how colonization rates vary as a function of habitat occupancy. A concerted analysis of existing data is needed to define and parameterize such colonization functions. Such an analysis can determine

the extent to which reduced colonization at low habitat occupancy heightens metapopulation extinction.

Literature Cited

Aizen, M. A., and P. Feinsinger. 1993. Forest fragmentation, pollination, and plant reproduction in a Chaco dry forest, Argentina. Ecology 75:330–351.

Allee, W. C. 1931. Animal aggregations: a study in general sociology. University of Chicago Press, Chicago.

Caughley, G. 1994. Directions in conservation biology. Journal of Animal Ecology 63:215–244.

Dennis, B. 1989. Allee effects: population growth, critical density, and the chance of extinction. Natural Resource Modeling 3:481–538.

Gaines, M. S., and L. R. McLenaghan. 1980. Dispersal in small mammals. Annual Review of Ecology and Systematics 11:163–196.

Gilpin, M., and I. Hanski. 1991. Metapopulation dynamics: brief history and conceptual domain. Academic Press, London.

Gurney, W. S. C., and R. M. Nisbet. 1978. Single species population fluctuations in patchy environments. American Naturalist 112:1075–1090.

Gyllenberg, M., and I. Hanski. 1992. Single-species metapopulation dynamics: a structured model. Theoretical Population Biology 42:35–61.

Gyllenberg, M., I. Hanski, and A. Hastings. 1996. Structured metapopulation models. Pages 93–108 *in* I. Hanski and M. Gilpin, eds. Metapopulation biology: ecology, genetics and evolution. Academic Press, London.

Hammond, D. S. 1995. Post-dispersal seed and seedling dispersal in tropical dry forest trees after shifting agriculture, Chiapas, Mexico. Journal of Tropical Ecology 11:295–313.

Hanski, I. 1996. Metapopulation dynamics: from concepts and observations to predictive models. Pages 69–91 *in* I. Hanski and M. Gilpin, eds. Metapopulation biology: ecology, genetics and evolution. Academic Press, London.

Hanski, I., and M. Gilpin. 1996. Metapopulation biology: ecology, genetics and evolution. Academic Press, London.

Hanski, I., and M. Gyllenberg. 1993. Two general metapopulation models and the core-satellite species hypothesis. American Naturalist 142:17–41.

Hanski, I., and E. Ranta. 1983. Coexistence in a patchy environment: three species of *Daphnia* in rock pools. Journal of Animal Ecology 52:263–279.

Hanski, I., M. Kuussaari, and M. Nieminen. 1994. Metapopulation structure and migration in the butterfly *Melitaea cinxia*. Ecology 75:747–762.

Hanski, I., T. Pakkala, M. Kuussaari, and G. C. Lei. 1995*a*. Metapopulation persistence of an endangered butterfly in a fragmented landscape. Oikos 72:21–28.

Hanski, I., J. Poury, T. Pakkala, and M. Kuussaari. 1995*b*. Multiple equilibria in metapopulation dynamics. Nature (London) 377:618–621.

Hanski, I., A. Moilanen, and M. Gyllenberg. 1996. Minimum viable metapopulation size. American Naturalist 147:527–541.

Hansson, L. 1991. Dispersal and connectivity in metapopulations. Pages 89–103 *in* M. Gilpin and I. Hanski, eds. Metapopulation dynamics: brief history and conceptual domain. Academic Press, London.

Harrison, S. 1991. Local extinction in a metapopulation context: an empirical evaluation. Biological Journal of the Linnean Society 42:73–88.

———. 1994. Metapopulations and conservation. Pages 111–128 *in* P. J. Edwards, R. M. May, and N. R. Webb, eds. Large-scale ecology and conservation biology. Blackwell, Oxford.

Jennersten, O. 1988. Pollination in *Dianthus deltoides* (Caryophyllaceae): effects of habitat fragmentation on visitation and seed set. Conservation Biology 2:359–366.

Kareiva, P., and U. Wennergren. 1995. Connecting landscape patterns to ecosystem and population processes. Nature (London) 373:299–302.

Kunin, W. E. 1993. Sex and the single mustard: population density and pollinator behavior effects on seedset. Ecology 74:2145–2160.

Kunin, W. E., and Y. Iwasa. 1996. Pollinator foraging strategies in mixed floral arrays: density effects and floral constancy. Theoretical Population Biology 49:232–263.

Lamont, B. B., P. G. L. Klinkhamer, and E. T. F. Witkowski. 1993. Population fragmentation may reduce fertility to zero in *Banksia goodii:* a demonstration of the Allee effect. Oecologia (Berlin) 94:446–450.

Lande, R. 1987. Extinction thresholds in demographic models of territorial populations. American Naturalist 130:624–635.

Lande, R., D. W. Schemske, and S. T. Schultz. 1994. High inbreeding depression, selective interference among loci, and the threshold selfing rate for purging recessive lethal mutations. Evolution 48:965–978.

Lawton, J. H., S. Nee, A. J. Letcher, and P. J. Harvey. 1994. Animal distributions: patterns and processes. Pages 41–58 *in* P. J. Edwards, R. M. May, and N. R. Webb, eds. Large-scale ecology and conservation biology. Blackwell, Oxford.

Levins, R. 1969. Some demographic and genetic consequences of environmental heterogeneity for biological control. Bulletin of the Entomological Society of America 15:237–240.

———. 1970. Extinction. Pages 77–107 *in* M. Gerstenhaber, ed. Some mathematical problems in biology. American Mathematical Society, Providence, R.I.

Lewis, M. A., and P. Kareiva. 1993. Allee dynamics and the spread of invading organisms. Theoretical Population Biology 43:141–158.

Loxdale, H. D., J. Hardie, S. Halbert, R. Footie, N. A. C. Kidd, and G. I. Carter. 1993. The relative importance of short- and long-range movement in flying aphids. Biological Reviews 68:291–311.

May, R. M. 1974. Stability and complexity in model ecosystems. Princeton University Press, Princeton, N.J.

Nee, S. 1994. How populations persist. Nature (London) 367:123–124.

Nee, S., R. M. May, and M. P. Hassell. 1996. Two species metapopulation models. Pages 123–146 *in* I. Hanski and M. Gilpin, eds. Metapopulation biology: ecology, genetics and evolution. Academic Press, London.

Peltonen, A., and I. Hanski. 1991. Patterns of island occupancy explained by colonization and extinction rates in shrews. Ecology 72:1698–1708.

Ray, C., M. Gilpin, and A. T. Smith. 1991. The effect of conspecific attraction on metapopulation dynamics. Biological Journal of the Linnean Society 42:123–134.

Robinson, J. G. 1988. Demography and group structure in the wedge-capped capuchin monkeys, *Cebus olivaceous.* Behaviour 104:202–231.

Shaffer, M. L. 1987. Minimum viable populations: coping with uncertainty. Pages 69–86 *in* M. E. Soule, ed. Viable populations for conservation. Cambridge University Press, Cambridge.

Sjogren P. 1991. Extinction and isolation gradients in metapopulations. The case of the pool frog (*Rana lessonae*). Pages 135–147 *in* M. Gilpin and I. Hanski, eds. Metapopulation dynamics: brief history and conceptual domain. Academic Press, London.

Small, R. J., J. C. Holzwart, and D. H. Rusch. 1993. Are ruffed grouse more vulnerable to mortality during dispersal. Ecology 74:2020–2026.

Smith, A. T., and M. M. Peacock. 1990. Conspecific attraction and the determination of metapopulation colonization rates. Conservation Biology 4:320–323.

Svane, I. 1984. Observations on the long-term population dynamics of the perennial ascidian, *Ascidia mentula* O. F. Muller, on the Swedish west coast. Biological Bulletin (Woods Hole) 167:630–646.

Thiollay, J. M., and B. U. Meyburg. 1988. Forest fragmentation and the conservation of raptors: a survey on the island of Java (Indonesia). Biological Conservation 44:229–250.

Thomas, C. D. 1994. Local extinctions, colonizations and distributions: habitat tracking by British butterflies. Pages 319–336 *in* S. R. Leather, A. D. Watts, N. J. Mills, and K. F. A. Walters, eds. Individuals, populations and patterns in ecology. Intercept, Andover.

Thomas, C. D., and I. Hanski. 1996. Butterfly metapopulations. Pages 359–386 *in* I. Hanski and M. Gilpin, eds. Metapopulation biology: ecology, genetics and evolution. Academic Press, London.