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ESTIMATING POSTNATAL DISPERSAL: TRACKING THE UNSEEN DISPERSERS

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Abstract. Postnatal dispersal, defined as dispersal from the natal patch soon after reaching maturity, is common in a variety of insect species. Postnatal dispersal may increase connections among subpopulations and, thus, significantly affect local population dynamics in metapopulation and source–sink contexts. Yet most mark–recapture studies of insects miss the postnatal dispersal phase because it comes soon after eclosion. *Cephaloleia fenestrata* (Chrysomelidae) is a specialist herbivore of the rolled leaves of *Pleiostachya pruinosa* (Marantaceae, common name ''prayer plant''). Some *P. pruinosa* patches were flooded prior to the onset of this study, extirpating the majority of *C. fenestrata* in the flood zone and providing a natural experiment and an opportunity to observe recolonization dynamics. We built a spatially explicit population projection matrix model to simulate spatial population dynamics of *C. fenestrata*. The model was a poor fit to the empirical data. Adding postnatal dispersal to the model resulted in a much better model fit. This study suggests that 81% of *C. fenestrata* disperse from the natal site soon after eclosion. Model simulations indicated that postnatal dispersal increases the mean population size in the flood zone more than six-fold and the standard deviation more than three-fold. Herein we present an implicit method of estimating postnatal dispersal when marking animals before the postnatal dispersal phase is problematic.

Key words: Cephaloleia fenestrata; *Chrysomelidae; emigration; flooding; Hispinae; immigration; population projection matrix model; postnatal dispersal; source–sink dynamics.*

INTRODUCTION

Many adult insects exhibit a strong propensity to disperse from their natal sites soon after maturation (Gatehouse and Zhang 1995), herein termed ''postnatal dispersal.'' Postnatal dispersal, as we define it, is inclusive of both ''natal dispersal,'' which is pre-breeding dispersal from the natal site (Gatehouse and Zhang 1995), and post-breeding dispersal from the natal site soon after reaching maturity. Patterns of postnatal dispersal vs. subsequent dispersal events may differ within a species (Greenwood 1983), thus indicating a need for separate estimates of the two when considering spatial population dynamics. The potential advantages of dispersal to animals are numerous: individuals may disperse to reduce resource competition (McCarthy 1999), avoid enemies (van Nouhuys and Hanski 2002), avoid inbreeding depression (Pusey and Wolf 1996), or ''hedge bets'' by spreading offspring across a landscape (Friedenberg 2003). On a regional scale, dispersal is important in that it can stabilize populations that would otherwise undergo population explosions and extinctions (Lecomte et al. 2004), possibly increasing local population persistence times. In a source–sink context, dispersal is key to maintaining elevated population densities in the sink habitat (Pulliam 1988). Thus, understanding postnatal dispersal may be critical to understanding source–sink dynamics.

In a review of studies that examined the reproductive status of migrating insects, Gatehouse and Zhang (1995) found that 28 out of 29 species engaged in pre-reproductive migration out of the natal patch. Measuring postnatal dispersal in insects is problematic, however, because it is difficult (if not impossible) to apply unique marks that will endure from the larval to the adult stage, and individuals in the adult stage are ''available'' for marking for only a short time before postnatal dispersal; thus, most newly eclosed adults undergoing postnatal dispersal will do so before being marked. For this reason, postnatal dispersal may be largely missed in mark–recapture studies of insects, and thus, inter-patch connectivity may be underestimated.

In this study we introduce a method of implicitly measuring postnatal dispersal in a Neotropical beetle, *Cephaloleia fenestrata* Weise, by tracking the beetle's colonization of previously unoccupied habitat. When movement of pre-breeders is unobserved in mark–recapture data, implicit measures of postnatal dispersal are necessary. In a previous study, Johnson (2004*b*) used mark–recapture data to estimate dispersal of *C. fenestrata*. Herein we describe a method of inferring the postnatal dispersal pattern of *C. fenestrata* by the post-hoc fitting of a spatially explicit population projection matrix model to empirical colonization data.

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The model includes a hybrid of age- and stage-specific within-patch transition probabilities for *C. fenestrata* and includes dispersal probabilities of both newly eclosed beetles (postnatal dispersal) and adults over 25 d old. This inference is possible because prior to the study a flood completely inundated a subset of host plant patches in sink habitat, extirpating nearly all adults (survival probability = 0.09) and larvae (survival probability = 0.00) of *C. fenestrata* in the flood zone (Johnson 2004*b*). Because the development time of immature *C. fenestrata* is approximately 5 mo (Johnson 2004*a*), we could be confident that adults found in the flood zone within 5 mo following a flood were immigrants from the source habitat and not recruits, so recruitment did not confound the results. The goals of this study were to determine whether *C. fenestrata* has a postnatal dispersal phase and to quantify the dispersal probability associated with it. We also demonstrate that postnatal dispersal is key to rapid recolonization of flooded habitat and elevated population sizes in this sink habitat.

METHODS

Study system

Cephaloleia fenestrata is a specialist herbivore on a patchily distributed plant in the family Marantaceae, *Pleiostachya pruinosa* (Regal) K. Schum., at La Selva Biological Station in the lowland wet forest of Costa Rica. *C. fenestrata* adults feed primarily in the approximately 1 m long immature rolled leaves of *P. pruinosa*, while the larvae feed primarily on the petioles of mature (unrolled) leaves. The larvae are rather sedentary while the adults are winged and are the dominant dispersal stage (Johnson 2004*a*). The rolled leaves remain available to *C. fenestrata* adults for approximately 2 d before they unroll, forcing the adults to either locate a new rolled leaf or move to the secondary feeding sites on the leaf petioles (Johnson 2004*a*). The patches of *P. pruinosa* range greatly in size from 1 to 735 ramets (D. M. Johnson and C. C. Horvitz, *unpublished manuscript*). A patch is defined as a group of ramets that are more than 17 m away from the nearest conspecifics (beyond this distance, interpatch movement is below 10% per 25 d [Johnson 2003]). This study includes 75 patches of *P. pruinosa* distributed over a somewhat linear 1.5 km long area near the Puerto Viejo River. The *P. pruinosa* patches are highly fragmented, encompassing less than 1% of the total study area (D. M. Johnson, *personal observation*). We are confident that the vast majority of patches in the study area were accounted for in the study. Seventeen of the 75 patches were located in the flood zone of the river. The flood zone population is a sink for *C. fenestrata*, while the population in the upland habitat acts as a source (Johnson 2004*b*). Patches in the flood zone were completely inundated by flooding of the river in January 1999, approximately one month before the first sampling period of this study. The river floods approximately once per year (Johnson 2004*a*).

Beetle sampling

To estimate adult beetle population size following the flood, we sampled patches of *P. pruinosa* from January 1999 to November 1999 with 12 sample periods approximately 25 d apart. During each sampling period all 75 patches were sampled. All rolled leaves with a diameter of 2 cm or greater at the apex were gently opened, and the number of *C. fenestrata* were recorded. Beetles were returned to the leaves, and the leaves were carefully re-rolled to minimize disturbance.

Population projection matrix model

We built a spatially explicit structured population model to describe the population dynamics of *C. fenestrata* across all of the host patches. The model is composed of both within- and among-patch dynamics. We begin with a structured population model for within-patch population dynamics (**W**). This population projection matrix is a hybrid between a Leslie and a Lefkovitch matrix, which combines an age-structured and a stage-structured matrix where the sub-diagonal is composed of nonzero values (see Appendix A for the structure of matrix model **W**). There are seven stages in this model: eggs, four age classes of larvae, pupae, and breeding adults. Surviving adult beetles remain in the adult stage, with a probability given by the product of the probability of survival (S_A) and the probability of the beetle not emigrating out of the patch over one time step. The adult stage is the only reproductive stage, as indicated by the only nonzero value on the first row of the matrix (R). The parameters S_E, S_L, S_P, and S_A are the survival probabilities per time step of eggs, larvae (the four age classes are assumed to have the same survival), pupae, and breeding adults, respectively. The parameter ρ is the probability of natal dispersal, thus $1 - \rho$ is the probability that there is no natal dispersal. The parameter ε_j is the probability of adult dispersal or emigration out of patch j, thus $1 - \varepsilon_j$ is the probability that breeding adults stay in patch j. There is one such matrix for each of the 75 patches in the study.

Each matrix that shows the probability of movement of each of the seven stages from one patch (patch j) to another (patch i) is signified as matrix $\mathbf{T}_{ij}$ and is composed of zeros except for the pupal-to-adult and adult-to-adult transitions (see Appendix A for structure of matrix $\mathbf{T}_{ij}$). Because this is a spatially explicit model, the values of the two nonzero movement parameters in each $\mathbf{T}_{ij}$ may vary depending upon each combination of source and target patch, where j is the source patch and i is the target patch. There is one such matrix of interpatch movements for each combination of source and target patch in the study ($75^2 - 75 = 5550$ matrices). Because natal dispersal could not be measured directly, it was necessary to make certain assumptions. The probability of postnatal emigration out of a patch (ρ) we assume to be an intrinsically driven behavior; thus, we modeled it as being independent of patch size. Postnatal immigration, however, is assumed to be equally dependent on patch size as in subsequent immigration because we reason that large patches are easier to find than small patches (Kareiva 1985) for beetles dispersing from the natal patch and other patches alike. Also, because both types of dispersers are adults with functioning wings, we made the reasonable assumption that the same dispersal kernel applied to both postnatal and breeding dispersers.

In modeling emigration and immigration by breeding adults, we followed the standard equations presented by Hanski et al. (2000). The probability of emigration out of a patch is described by the equation

$$\varepsilon_j = \min(1, \eta A_j^{\zeta_{\mathrm{em}}}) \tag{1}$$

in which A is patch size measured as the number of ramets, ζ_{em} is a patch size-dependent emigration parameter, and η is the probability of a beetle dispersing from a patch one ramet in size over one time step (25 d). In this model the probability of emigration decreases as patch size increases. The redistribution of both postnatal and subsequent dispersers is described by the immigration equation

$$\iota_{ij} = \frac{d_{ij}^{-\alpha} A_i^{\zeta_{\mathrm{im}}}}{\sum_{i=1}^{n} (d_{ij}^{-\alpha} A_i^{\zeta_{\mathrm{im}}})} \tag{2}$$

in which d is the Euclidean distance between patches i and j, α is the dispersal kernel power function, A is patch size, and ζ_{im} is the patch size-dependent immigration parameter. In Eq. 2, large patches attract more immigrants than small patches. This equation differs from that of Hanski et al. (2000) in that the dispersal kernel is a power decay function rather than an exponential decay function. We selected the power decay function over the exponential decay function because it was a better describer of regional population dynamics of *C. fenestrata* (Johnson 2003).

We next assembled the 75 matrices for population dynamics within each patch ($\mathbf{W}_{ii}$) and the 5550 matrices for spatially explicit movements between patches ($\mathbf{T}_{ij}$). In the complete spatially explicit matrix ($\mathbf{M}$), within-patch dynamics are on the diagonal and among-patch dynamics are in the other areas of the matrix (see Appendix A for a visualization of the matrix structure). Two such matrices were created, both supported by empirical data, one for non-flood periods ($\mathbf{M}_{\mathrm{nf}}$) and one for flood periods ($\mathbf{M}_{\mathrm{f}}$).

We projected the spatial population dynamics using the matrices $\mathbf{M}_{\mathrm{f}}$ and $\mathbf{M}_{\mathrm{nf}}$ in a particular temporal sequence as described below to make quantitative predictions of population dynamics of beetles in the flood zone after the January 1999 flood. In a previous study, Johnson (2004*b*) determined that a large majority of adults and virtually all larvae were killed by flooding, thus the population dynamics within the flood zone following a flood is dominated by immigration from the upland habitat. The simulation was run on a cycle in which there was a flood event every 14 time steps (approximately 1 yr), similar to that observed (Johnson 2004*b*). The model was run for 1400 time steps to allow the simulated population to settle into a non-transient pattern of sustained cycles in both the upland and the flood zone (Appendix B illustrates that far less than 700 time steps would have been sufficient to approximate non-transient dynamics). To evaluate whether differences between model predictions and empirical data could be explained by variation in parameter estimates, we varied model parameters one at a time to reasonable levels (95% CI) and reran the model. See Appendix C for description and detailed results of the sensitivity analyses.

We implicitly measured postnatal dispersal by fitting the postnatal emigration probability parameter ρ to the empirical data by minimizing the sum of squares of differences between the observed and predicted beetle population sizes in the flood zone through the first seven sample periods following a flood. This is a deterministic matrix model with beetle densities equal to zero in the flood zone patches and proportional to patch size in the upland patches at initial conditions. Only the first seven sampling periods were used to avoid the confounding effects of changes in habitat quality on immature survival. The development of *C. fenestrata* from egg to adult is approximately seven time steps (175 d; Johnson 2004*a*).

Lastly, we simulated population dynamics of *C. fenestrata* over 1000 time steps with stochastic flood events occurring at a probability of 0.07 per time step (equal to approximately once per year as was determined in Johnson [2004*b*]). The model was simulated twice, once with and once without postnatal dispersal. We compared the means and standard deviations of the population densities in the flood zone over the final 200 time steps to assess the effects of postnatal dispersal on the population dynamics of *C. fenestrata* in the flood zone (a sink population).

RESULTS

The migration-related parameters were estimated in a concurrent study (Johnson 2003) and are provided in Appendix C. Model simulations without postnatal dispersal underestimate the observed numbers of adult beetles recolonizing the flood zone following a flood by 86% (Fig. 1A). Neither changing model parameter values to their 95% confidence limits nor 2 SE changes in the population growth rate were sufficient to explain the discrepancy between the empirical data and model predictions of the number of recolonizers of the flood zone (Appendix C, and see the comparison between

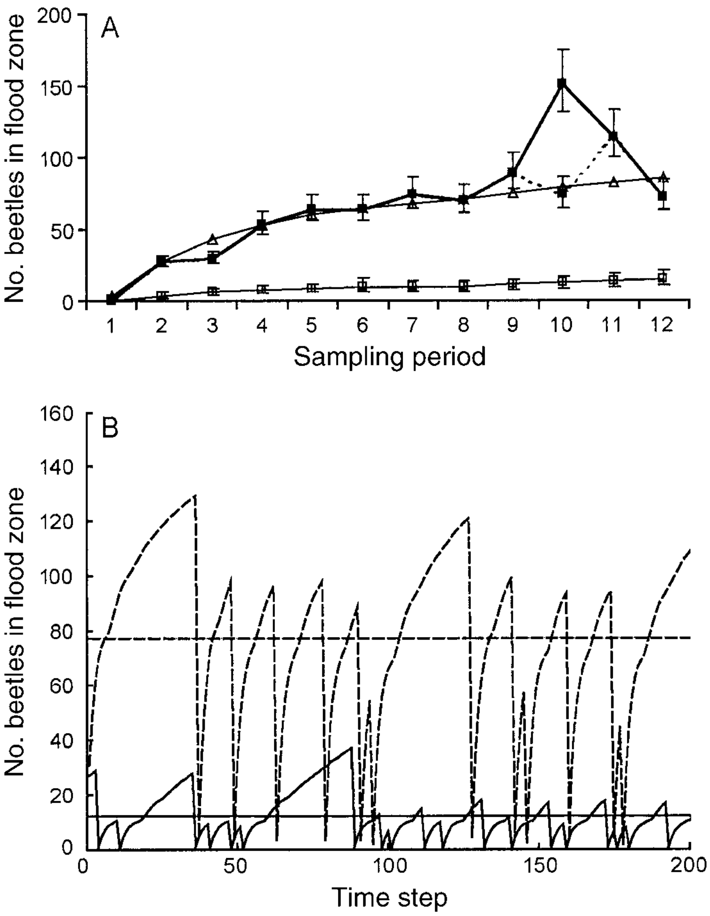

FIG. 1. (A) Comparison of the estimated number of *Cephaloleia fenestrata* beetles in the flood zone from empirical data (thick line, solid squares), the model without postnatal dispersal (open squares), and the model with 81% natal dispersal (open triangles). The dotted line is the empirical data with the outlier removed from the 10th and 11th sampling periods. Error bars on the model without postnatal dispersal are the maximum and minimum change in the estimate (1) when the parameters patch size-dependent immigration and emigration (ζ_{im} and ζ_{em}, respectively), dispersal kernal power function (α), probability of a beetle dispersing from a patch one ramet in size over one time step (η), survival probabilities per time step (for eggs, pupae, and breeding adults in the flood and nonflood zones: S_E, S_P, $S_{A,f}$, $S_{A,nf}$, respectively), and population growth rate (λ) are set at their 95% confidence intervals one at a time; (2) when survival probability per time step of larvae (S_L) is varied at a reasonable level; and (3) when migration from outside the study area is included in the model (see Appendix C for detailed sensitivity analysis); thus, parameters were varied separately, not in concert. The error bars on the empirical estimation indicate the 95% confidence interval. (B) Simulated population dynamics of *C. fenestrata* in the flood zone with stochastic flood events occurring with a probability of 0.07 per time step (once per year), with (fluctuating dashed line) and without (fluctuating solid line) postnatal dispersal. The horizontal dashed line indicates the mean population size with postnatal dispersal (77, SD = 31), and the horizontal solid line indicates the mean population size without postnatal dispersal (12, SD = 8).

the predicted number of beetles recolonizing the flood zone [and 95% error bars] without postnatal dispersal [open squares] vs. empirical data [closed squares] in Fig. 1A). Changing ζ_{em} to its lower 95% confidence value had the greatest effect, but the model still underestimated beetle numbers in the flood zone by 82%. Changing the survivorship parameters of eggs and pupae (S_E and S_P) to non-flood survivorship levels had a minimal effect on predicted recolonization, still underestimating observed beetle numbers by 81%. Varying the population growth rate to between 0.90 and 1.14 (2 SE variation [Johnson 2004*b*]) had little effect on recolonization of the flood zone, still underestimating recolonization rate by 82–90%. In a previous study, Johnson (2003) estimated remote migration of *C. fenestrata* into the study area to be 2.46 individuals per 6 mo. Adding remote migration to the model, however, had little effect of the recolonization rate of the flood zone, still underestimating it by 86%. Thus, sensitivity analyses demonstrated that reasonable variation in these above parameters, the population growth rate, and remote migration were not sufficient to explain the observed rapid recolonization of the flood zone.

When postnatal dispersal was added to the model ($\rho > 0$ in Eqs. 1 and 2), however, it predicted the observed number of beetles in the flood zone following a flood reasonably well, at least through the eighth or ninth sampling periods (compare open triangles to closed squares in Fig. 1A). The best fit of the model through the seventh sampling period had a postnatal dispersal probability of 81% ($\rho = 0.81$). This measure of ρ was somewhat sensitive to variation in the model parameters, but was still estimated to be at an elevated level, where 95% CI variation in α induced that greatest variation in estimates of ρ, ranging from 58% to 100% (Appendix C). Seven sampling periods were chosen because the eighth sampling period is when we would expect eggs laid after the flooding to emerge as adults, and thereby recruits from the flood zone would confound the data. This model failed to predict the large increase in the number of beetles between the ninth and 10th sampling periods in the empirical data (compare open triangles to closed squares in Fig. 1A). Rerunning parameter estimation assuming an exponential decay dispersal kernel resulted in a somewhat lower estimate of $\rho = 0.49$ (Appendix C). Making the assumption that postnatal dispersal was dependent on patch size resulted in a 34% underestimate of flood zone recolonization even when ρ was set at a maximum probability $= 1$ (Appendix C).

Simulations of the model with stochastic flooding events indicate that fluctuations in population size in the flood zone are driven by the flood events (Fig. 1B). In the model with postnatal dispersal, *C. fenestrata* had a mean population size over six-fold higher than in the model without postnatal dispersal (77 vs. 12 beetles, respectively). The magnitude of the variation in population size was over three times greater in the model with postnatal dispersal than in the model without (standard deviations equal to 31 vs. 8, respectively).

DISCUSSION

The January 1999 flood of the Puerto Viejo River provided an excellent opportunity to measure postnatal dispersal in *C. fenestata* by studying the beetles' recolonization dynamics in the flood zone. The model parameterized from the mark–recapture study greatly under-predicted the recolonization rate in the flood zone, even with 95% confidence interval changes to model parameters. When 81% postnatal dispersal was added to the model (compared to a previous estimate of 9% adult dispersal per 25 d [Johnson 2003]), it was a good fit to the empirical data, through the sampling period at which we could be confident that nearly all new beetles were immigrants and not recruits.

Strategies for postnatal dispersal can take one of three general forms in insects. First, individuals may show a propensity for dispersal from the natal patch in the absence of any morphological or physiological differences from the non-dispersers (Dingle 1996). Second, in some winged insects, histolysis of wing muscle occurs after dispersal events, with the energy gain being diverted toward reproductive output, a process known as oogenesis-flight syndrome (Johnson 1969). In support of the oogenesis-flight syndrome, trade-offs between oogenesis and flight ability have been demonstrated in insects such as a sand cricket (Mole and Zera 1994) and a cuculionid beetle (Rankin et al. 1994). Whether *C. fenestrata* exhibits oogenesis-flight syndrome is unknown; however, because *C. fenestrata* is long-lived (adults live up to at least 9 mo) and lives in a highly fragmented habitat where they must repeatedly disperse to new rolled leaves on the order of every 2 d (Johnson 2004*a*), we reason that it is unlikely that histolysis of wing muscles would be advantageous to *C. fenestrata*. Third, some insects display bimodality in morphological traits associated with migration (i.e., long-winged vs. flightless individuals), in which a higher proportion of winged individuals may be produced under high density conditions to facilitate dispersal from the natal patch, perhaps to avoid competition (Denno and Roderick 1992). While we did not test for wing dimorphism in *C. fenestrata*, we feel this syndrome is also unlikely because there is no evidence for competition in the guild of rolled leaf beetles (Strong 1982).

Because we find the possibilities of the oogenesis-flight syndrome unlikely, we assumed that dispersal distance from the natal patch was similar to subsequent dispersal distances. In general, postnatal dispersal distances are usually longer than subsequent dispersal distances in birds (Greenwood 1983), although whether this is generalizable to terrestrial insects is unclear. If postnatal dispersal distances are greater than subsequent dispersal distances in *C. fenestrata*, then an 81% probability of postnatal dispersal may be an overestimation because longer dispersal distances would mean that fewer dispersal events would be necessary for a certain number of beetles to disperse from the upland to the flood zone. However, sensitivity analysis indicates that the recolonization rate is not overly sensitive to changes in the dispersal kernel parameter (α) (Appendix C). Thus, this study suggests that *C. fenestrata* has a significant postnatal dispersal phase.

In a source–sink context, we demonstrated that postnatal dispersal could have large effects at increasing beetle density in the sink habitat. This certainly is not a surprise as a fundamental tenet of source–sink theory is that directional dispersal from a source habitat sustains population size in a sink habitat either above extinction (Pulliam 1988) or elevated above a non-zero equilibrium in the case of a pseudo-sink (Watkinson and Sutherland 1995). In the models with postnatal dispersal, greater dispersal from the upland caused greater explosions and crashes in population size in the flood zone, thus opposite to the predicted effect of dispersal tempering population explosions (Lecomte et al. 2004). However, this effect is easily understood when one considers that greater dispersal into the flood zone simply results in larger population sizes that will eventually crash due to the next flood event.

In the 10th sampling period, the empirical estimate of the number of beetles in the flood zone exceeded the model prediction by 91% (compare open triangle and solid square in Fig. 1A). There are two possible explanations for the divergence. First, the divergence coincides with the time when eggs laid in the flood zone after the flood would become adults. Thus, previously flooded patch may provide some delayed advantage to *C. fenestrata* through top-down effects such as reducing parasitoid numbers, bottom-up effects such as improving host-plant quality, or by inducing higher rates of egg-laying by adults. Alternatively, the divergence may have been caused by an abnormal event in a single patch, where nearly half of the beetles in the flood zone during the 10th sampling period occurred in just one of the 17 patches. When this ''outlier'' is removed from the analysis, the model is a better fit (indicated by the dashed-line in Fig. 1A).

This study demonstrated that postnatal dispersal was an important factor in the spatial population dynamics of *C. fenestrata*, causing elevated population sizes in a sink habitat. In fact, postnatal dispersal may very well be prevalent in insects in general (Gatehouse and Zhang 1995), yet measuring postnatal dispersal in insects is problematic. Lebreton et al. (2003) introduced a method for estimating natal dispersal when nonbreeders are marked at birth, but are unobservable until the breeding phase. The Lebreton et al. method, thus, is useful when marks on immatures are retained into adulthood. Indeed, high levels of natal dispersal also appear to be common in birds (Greenwood and Harvey 1982) as well as insects. The reason for dispersal from the natal patch in vertebrates and insects may be different, however, because vertebrates may disperse for reasons of territoriality (Ims and Andreassen 1991), while territoriality in insects is less common (but see Mason [1996] for an example). Still, the ultimate cause of each may be to reduce competition and/or inbreeding depression. Whatever the reason for postnatal dispersal, understanding dispersal rates is important because they in turn influence the stability of spatially structured populations (Rolf 1975), metapopulations (Huffaker 1958), and source–sink systems (Holt 1985).

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APPENDIX A

A population projection matrix model is available in ESA's Electronic Data Archive: *Ecological Archives* E086-065-A1.

APPENDIX B

A figure presenting predicted population dynamics in the upland and flood zone in the simulation model is available in ESA's Electronic Data Archive: *Ecological Archives* E086-065-A2.

APPENDIX C

A description of the sensitivity analyses, the effects of variation in model parameters and model assumptions on recolonization rate in the flood zone, is available in ESA's Electronic Data Archive: *Ecological Archives* E086-065-A3.