

Changes in landscape structure decrease mortality during migration

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Received: 9 November 2005 / Accepted: 22 June 2006 / Published online: 21 July 2006
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Abstract I examined the dispersal of the red milkweed beetle, *Tetraopes tetraophthalmus*, among patches of its host plant, common milkweed, *Asclepias syriaca*. Over a 5-year period, the number of patches in a landscape and their mean size increased, while the distance between patches decreased. Over the same period the proportion of beetles dispersing between patches increased from 0.48 to 0.62. Estimates from the virtual migration model showed that mean migration distance decreased from 158 to 72 m for male beetles and from 129 to 72 m for female beetles. Estimated mortality per migration event decreased as the landscape changed, but was low in all years. The estimated mean migration mortality per patch decreased from 1.45×10^{-2} to 3.70×10^{-7} for male beetles. Female migration mortality decreased from 5.48×10^{-3} to 3.88×10^{-6} . Increasing the size and number of patches and decreasing interpatch distance decreases migration mortality and may play an important role in the conservation of species, particularly where mortality during dispersal is high.

Keywords *Asclepias* · Connectivity · Dispersal · Immigration · Milkweed

Introduction

Many habitats and the populations which reside in them are spatially segregated. Habitat segregation can occur naturally when resources are heterogeneously distributed across a landscape and can arise through anthropogenic processes such as habitat fragmentation. Understanding how populations respond to spatial heterogeneity in habitat structure is of basic interest for ecology (Pulliam 1988; Hanski 1999) and is broadly applicable to conservation, planning, and remediation (Debinski and Holt 2000; Cabeza and Moilanen 2003).

The migration of organisms is central to determining how populations respond to spatial segregation. When migration among habitat patches is frequent, a network of patches functions as one large population. When migration is moderate, local populations can have independent local dynamics united to varying degrees by the amount of migration among them (Hastings and Harrison 1994). More migration among populations generally produces greater synchrony among the dynamics of local populations (Hanski and Woiwood 1993; Matter 2001a). If migration among habitats is infrequent, groups of populations may function as a metapopulation where colonization and extinction processes dominate the spatial dynamics (Hanski 1999). Other types of spatial dynamics can exist within this continuum such as source–sink dynamics where certain populations are net exporters of migrants while others are dependent on immigration for their persistence (Pulliam 1988; Thomas et al. 1997).

The theoretical study of spatial population dynamics and migration has advanced relatively quickly; however, empirical study has lagged largely due to the difficulty in obtaining sufficient, high-quality data for

Communicated by Scott Robinson

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migration (Bowne and Bowers 2004). One important, yet difficult to estimate, aspect of migration is the mortality that occurs during migration events. This source of mortality has a direct effect on regional population growth and dynamics as well as important implications for metapopulation persistence (Hanski 1999; Baguette et al. 2003; Hudgens and Haddad 2003), community structure (Amarasekare et al. 2004), and the evolution of dispersal strategies (Gandon and Michalakis 1999).

It is generally assumed that migration mortality increases with increasing habitat fragmentation and interpatch distance. The risk of mortality is thought to increase with the amount of time that an individual spends migrating. Because it takes longer to travel farther, migration mortality should increase with increasing interpatch distances. It is also widely assumed that many of the negative aspects of habitat fragmentation, including increased migration mortality, can be ameliorated by facilitating migration among local populations (Simberloff et al. 1992; Hudgens and Haddad 2003). Increasing migration among populations should decrease the risk of metapopulation extinction by allowing more frequent recolonization and decreasing inbreeding depression (Saccheri et al. 1998; Hanski 1999). Despite the logic behind the assumptions surrounding mortality occurring during migration, empirical evaluations of how changes in landscape structure affect this source of mortality are lacking.

Here, I examine the migration of the red milkweed beetle, *Tetraopes tetraophthalmus* (Forster), among patches of its host plant, common milkweed, *Asclepias syriaca* L. Specifically I investigate how changes in landscape structure occurring over a 5-year period affect mortality occurring during migration.

Materials and methods

Study species

T. tetraophthalmus is a univoltine, monophagous herbivore of common milkweed, *A. syriaca*. Larval beetles feed underground on the roots and rhizomes of milkweed (Matter 2001b). The beetles pupate in the soil and adults emerge in rough synchrony with the flowering of milkweed (Hartman 1977; Matter et al. 1999). Adult beetles feed on the buds, flowers, and foliage of milkweed (Matter 2001b), spending a majority of time feeding and mating (McCauley and Lawson 1986). Females oviposit into hollow grass stems (Gardiner 1961; Agrawal 2004). Adult females can be distin-

guished from males by the presence of a suture on the ventral surface of the last segment that is absent in males (Chemsak 1963). These aposematically colored beetles sequester cardiac glycosides from their host plant and are unpalatable to vertebrate predators (Farrell 2001) but not to other arthropods (McCauley and Lawson 1986).

Local population size and rates of emigration and immigration of this beetle are a function of the size of patches of its host plant (Matter 1997). While the number of immigrants and emigrants increases with patch size, the intensity of immigration and emigration (number per unit patch size) decreases as patch size increases (Matter 1997). Immigration of this species is predicted well by models including both target patch size and species-specific interpatch distances (Matter et al. 2005). Several studies investigating the migration of this species have found that males tend to move farther and more frequently than females (McCauley et al. 1981; Lawrence 1982; Matter 1996).

A. syriaca is a clonal, perennial plant, commonly found in pastures and old fields in eastern North America (Wyatt et al. 1993). Its clonal nature results in a heterogeneous distribution with patches consisting of one individual (genet) ranging in size from one to several hundred ramets. Change in the size of patches occurs on an annual basis. Ramets are produced from belowground rhizomes each spring and senesce in the fall. Root herbivory by the beetles and competition with other plants reduces the growth of milkweed (Matter 2001b; Agrawal 2004).

Mark-recapture and study site

I conducted mark-recapture within a 40-ha meadow at the University of Virginia's Blandy Experimental Farm, Boyce, Virginia (Clarke County) USA. The meadow consisted primarily of bedstraw (*Galium verum*), honeysuckle (*Lonicera japonica*), several grasses (*Festuca* spp. and *Poa* spp.) and numerous patches of common milkweed. The meadow was pastured prior to 1983 and was burned or mowed, approximately every other year between 1984 and 1995, to reduce the number of woody plants. The meadow was isolated from other milkweed patches by over 700 m making the system fairly closed given that the mean lifetime distance moved by these beetles is less than 170 m (McCauley et al. 1981; Lawrence 1982; Matter 1996). *T. tetraophthalmus* do possess strong flight abilities (Davis 1981) and infrequently colonize patches isolated by up to 5 km (McCauley 1989). Thus, it is likely that a small number of beetles leave the system entirely and immigrate from patches outside of the system.

I identified all milkweed patches (a ramet separated by > 10 m from other ramets) and censused them for beetles during 1992 and 1995–1997. New patches arising during the study were also held to this criterion. Due to natural patch growth, some interpatch distances declined to less than 10 m. I used the number of ramets as a metric of patch size as it explains more variation in beetle abundance than does geometric area (Matter 1996). I counted the number of ramets for each patch, each year. In 1992, I used a transit and existing grid system within the meadow to determine the location of the center of each milkweed patch. In subsequent years, I determined patch locations with differentially corrected (± 1 m accuracy) GPS data.

I searched for beetles daily over the first 2 weeks of adult activity and approximately 3 times a week thereafter. Each newly captured beetle received a unique mark on its elytra using model enamel paint (Matter 1996). I recorded the sex, date, and location for all beetles captured, except for a few beetles captured initially in 1992 which were unsexed.

Modeling

To examine the migration of beetles and mortality occurring during migration, I used the virtual migration (VM) model (Hanski et al. 2000; Petit et al. 2001; Wahlberg 2002; Matter et al. 2004). The model makes several biological assumptions to estimate survival and migration among populations. The model is based on discrete events occurring on a daily basis. First, an individual survives in a patch with probability ϕ_p . Surviving individuals may either stay in a patch or emigrate. The probability of emigration is modeled as a function of patch size. Thus, the probability of an individual emigrating (ϵ) from patch j is related to its size (A_j) by the power function:

$$\epsilon_j = \eta A_j^{-\zeta_{em}}, \quad (1)$$

where $\eta > 0$ and $\zeta_{em} > 0$ describe emigration from a patch relative to unit size (one ramet) and the scaling of emigration with patch size, respectively. Emigrants survive migration with a patch-specific probability ϕ_{mj} , based on patch size and interpatch distances, and immigrate into a new patch within the same time interval.

In the context of modeling successful emigration, the connectivity, S_j , (note the inverse relationship between connectivity and interpatch distance) of patch j is a function of the distance ($d_{j,k}$) between patch j and k , the size of patch k , and how immigration scales with patch size (ζ_{im}):

$$S_j = \sum_{k \neq j} \exp(-\alpha d_{j,k}) A_k^{\zeta_{im}}. \quad (2)$$

The parameter α describes the species-specific effect of interpatch distance on migration. This definition of “connectivity” is a functional, patch-based metric, attempting to describe the number of immigrants that a particular patch receives (Hanski 1999; Moilanen and Nieminen 2002; Matter et al. 2005). It should not be confused with landscape scale “connectivity” which attempts to describe the ease with which organisms move through landscapes (Tischendorf and Fahrig 2000).

The probability of surviving migration (ϕ_{mj}) from patch j is a sigmoidally increasing function of its connectivity and the parameter $\lambda > 0$ which alters the shape of the curve:

$$\phi_{mj} = \frac{S_j^2}{\lambda^2 + S_j^2}. \quad (3)$$

Individuals that survive emigration from patch j are allotted to new patches according to the relative contribution of each patch to the connectivity of patch j . Thus, the probability of migrating from a particular patch j to a particular patch k ($\psi_{j,k}$) is:

$$\psi_{j,k} = \frac{\exp(-\alpha d_{jk}) A_k^{\zeta_{im}}}{\frac{\zeta_j}{S_j} + S_j}. \quad (4)$$

The VM model assumes that emigration and immigration are a function of patch size and that immigration is a declining function of interpatch distances. Data from 1992 meet these assumptions (Matter 1996, 1997), but the other years have not been fully examined. Matter et al. (2005) show that the connectivity metric used here, including target patch size and an exponentially decreasing dispersal distance, was the best predictor of the immigration of *Tetraopes* for the 1995–1997 data. However, to ensure that data met the assumptions of the VM model, I examined the proportion of beetles emigrating from and number of immigrants into each patch versus the size of that patch. I also examined the frequency of dispersal distances for the combined 1995–1997 data.

Parameters for the VM model were estimated separately for each sex of beetle in each year using maximum likelihood methods. Estimation was conducted using 1,000 randomizations in simulated annealing followed by 10,000 intelligent randomizations to converge on the optimum (Hanski et al. 2000). I assessed the fit of the model by comparing the observed numbers of

immigrants and emigrants for patch j at time t and time $t - 1$ to the expected numbers. The statistic, Q , was calculated summing across all time periods and patches. Goodness-of-fit tests assume a χ^2 distribution with df equal to the number of summands (Hanski et al. 2000).

Results

During the four field seasons (1992, 1995–1997), I captured a total of 5,305 individuals (2,580 males and 2,725 females) and recorded 3,070 migration events. The proportion of beetles emigrating decreased with patch size, although there was considerable variation particularly for small patches with small populations (Fig. 1). The number of immigrants into a patch increased with patch size (Fig. 2). It should be noted, however, that the intensity of immigration (number per unit patch size) decreased as patch size increased. The frequency of dispersal decreased with increasing interpatch distance (Fig. 3). These three results for

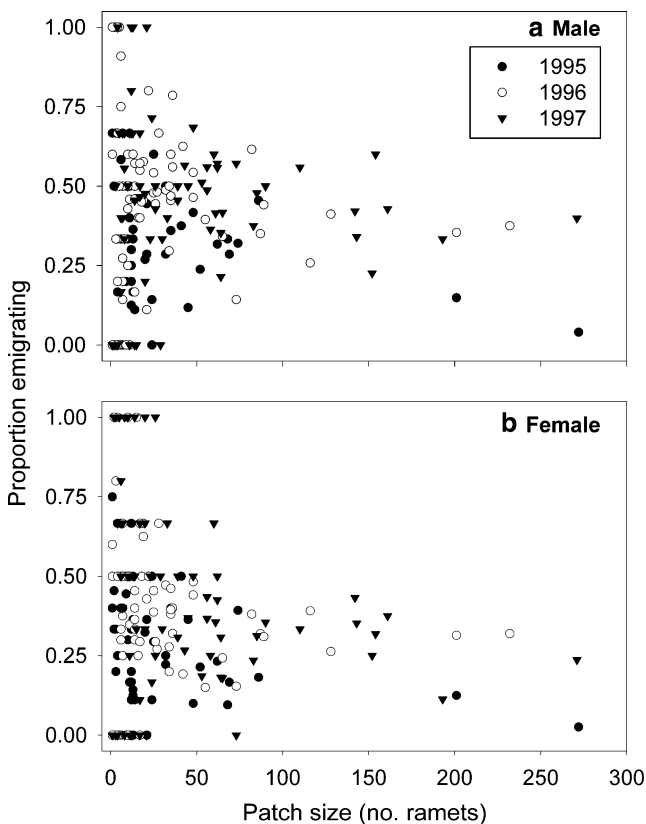


Fig. 1 The proportion of individual **a** male and **b** female *Tetraopes tetraophthalmus* that emigrated from a patch versus patch size (number of ramets, i.e., stems of a clonal plant). Data shown are for 1995 (filled circle), 1996 (open circle) and 1997 (inverted filled triangle). The largest patch in 1997 was omitted to provide more clarity

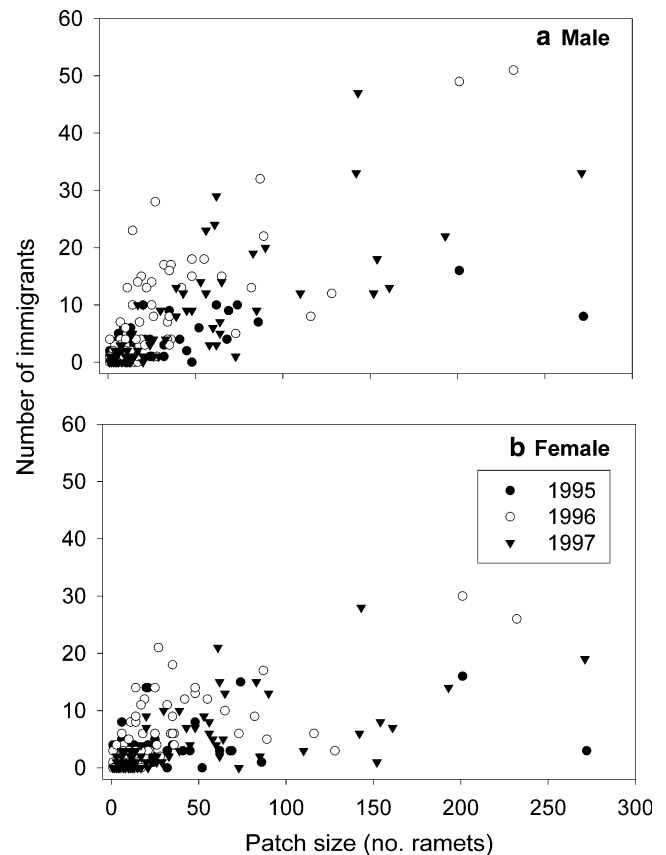


Fig. 2 The number of **a** male and **b** female *T. tetraophthalmus* that immigrated into a patch plotted versus patch size (number of ramets). Data shown are for 1995 (filled circle), 1996 (open circle) and 1997 (inverted filled triangle). Although the number of immigrants increases with patch size, the intensity of immigration (number per unit patch size) decreases. The largest patch in 1997 was omitted to provide more clarity

1995–1997 and the previous results of Matter (1996, 1997) demonstrate that the data meet the assumptions of the VM model.

Over the course of the study, due to natural processes, the size and number of milkweed patches in the landscape increased and the distance between patches decreased (Fig. 4). As the landscape changed, there were changes in the migration of beetles among patches. The proportion of beetles recaptured that moved between patches increased (0.48, 0.56, 0.66, and 0.62, for 1992 and 1995–1997, respectively) while the estimated mean migration distance ($1/\alpha$) decreased from 158 to 72 m for male beetles and from 129 to 72 m for female beetles (Table 1). Mean patch connectivity, as estimated by Eq. 2, increased from 3.61 ± 0.05 (SE) in 1992 to 141.04 ± 5.55 in 1997. Changes in both migration distance and connectivity are a function of changes in the landscape and the response of beetles to the landscape (Hanski et al. 2000). Estimated mortality per migration event decreased as the landscape changed

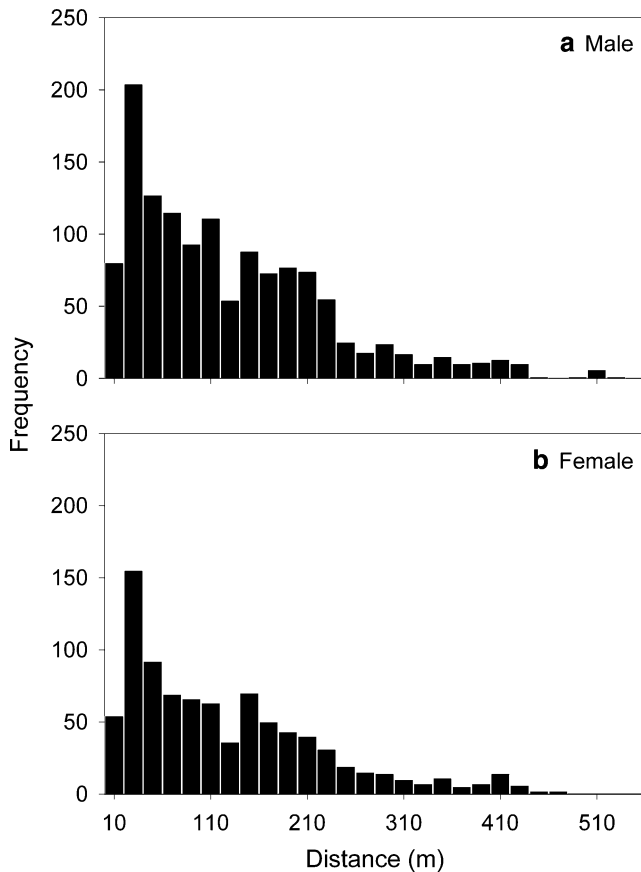


Fig. 3 The frequency of interpatch distances moved for individual **a** male and **b** female *T. tetraophthalmus* from 1995 to 1997. Note that the minimum interpatch distance was ~10 m, therefore there are relatively few movements in the 0- to 20-m class. X-axis labels indicate the midpoint of the interval

and was low in all years (Fig. 5). The estimated mean migration mortality per patch was $1.45 \times 10^{-2} \pm 4.95 \times 10^{-3}$, $8.86 \times 10^{-7} \pm 1.37 \times 10^{-7}$, $2.31 \times 10^{-7} \pm 8.10 \times 10^{-8}$, and $3.70 \times 10^{-7} \pm 5.16 \times 10^{-8}$ for male beetles in 1992 and 1995–1997, respectively. Females suffered greater migration mortality than males in 3 of the 4 years, and exhibited the same pattern as the landscape changed: $5.48 \times 10^{-3} \pm 2.07 \times 10^{-3}$, $6.48 \times 10^{-5} \pm 9.56 \times 10^{-6}$, $2.11 \times 10^{-6} \pm 9.00 \times 10^{-7}$, and $3.88 \times 10^{-6} \pm 5.39 \times 10^{-7}$. No statistical test was performed because these data are not independent, i.e., the same patch could be included in multiple years.

Because changes in landscape configuration also affected the amount of migration, the decrease in mortality per migration event could be offset by the increase in the amount of migration. One of every 93 male and one of every 313 female beetles died during migration using the respective mean patch connectivities for each sex seen in 1992. The decrease in mortality per migration more than offset the increase in the amount of migration. In 1997, using the respective mean connectivities in that year, only one of every 5.18 million male and one of 910,000 female beetles would have died during migration.

All models showed some lack of fit. Emigration for male beetles in 1992 ($\chi^2 = 88.67$, $df = 52$, $P = 0.001$) and in 1996 ($\chi^2 = 111.19$, $df = 71$, $P = 0.002$) showed significant lack of fit as well as immigration in all years, for both sexes in 1992 ($\chi^2 = 139.47$, $df = 61$, $P < 0.001$; $\chi^2 = 80.31$, $df = 52$, $P = 0.049$), 1995 ($\chi^2 = 123.41$, $df = 75$, $P < 0.001$; $\chi^2 = 100.63$, $df = 75$, $P = 0.026$),

Fig. 4 Changes in the size and number of milkweed (*Asclepias syriaca*) patches within the landscape during the study (**a** 1992, **b** 1995, **c** 1996, **d** 1997). The size of the circle is proportional to patch size (number of ramets). Note that some overlap occurs due to patch growth and because most patches are not circular

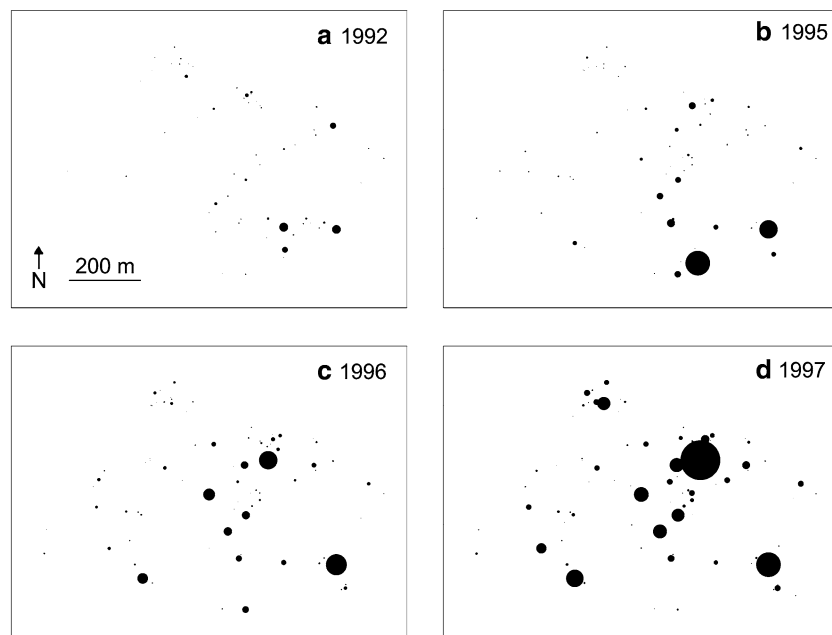


Table 1 Parameter estimates from the virtual migration model for *Tetraopes tetraophthalmus* (95% confidence intervals in parentheses, except for capture probability where variance is shown)

Parameter	1992		1995		1996		1997	
	Male (n = 676)	Female (n = 708)	Male (n = 676)	Female (n = 708)	Male (n = 676)	Female (n = 708)	Male (n = 676)	Female (n = 708)
Capture probability	0.202 (0.003)	0.247 (0.017)	0.386 (0.003)	0.374 (0.019)	0.365 (0.004)	0.383 (0.014)	0.374 (0.003)	0.360 (0.006)
α_m (distance dependence)	6.339 (4.571–8.164)	7.726 (5.561–9.770)	15.798 (13.466–18.219)	16.611 (14.449–18.903)	12.520 (11.208–13.726)	10.703 (9.318–12.117)	13.850 (12.552–15.326)	13.863 (12.210–15.671)
ϕ_p (within-patch survival)	0.939 (0.910–0.985)	0.912 (0.901–0.973)	0.860 (0.843–0.884)	0.913 (0.898–0.928)	0.929 (0.920–0.959)	0.927 (0.917–0.950)	0.926 (0.916–0.949)	0.940 (0.922–0.954)
χ^2 (migration mortality)	0.016 (0.000–0.042)	0.002 (0.000–0.027)	<0.001 (0.000–0.014)	0.031 (0.004–0.068)	0.002 (0.000–0.019)	0.009 (0.000–0.071)	0.004 (0.000–0.028)	0.039 (0.004–0.077)
η (emigration constant)	0.030 (0.014–0.068)	0.024 (0.011–0.076)	0.010 (0.005–0.0021)	0.005 (0.002–0.009)	0.040 (0.027–0.069)	0.022 (0.014–0.038)	0.011 (0.009–0.021)	0.012 (0.005–0.017)
ζ_{em} (scaling of emigration)	0.206 (0.105–0.313)	0.186 (0.070–0.317)	0.474 (0.357–0.591)	0.521 (0.435–0.630)	0.229 (0.148–0.302)	0.276 (0.194–0.354)	0.552 (0.440–0.599)	0.436 (0.366–0.594)
ζ_{im} (scaling of immigration)	0.849 (0.715–0.970)	0.746 (0.601–0.890)	0.621 (0.492–0.752)	0.487 (0.391–0.567)	0.790 (0.710–0.864)	0.648 (0.563–0.741)	0.685 (0.614–0.784)	0.676 (0.557–0.750)

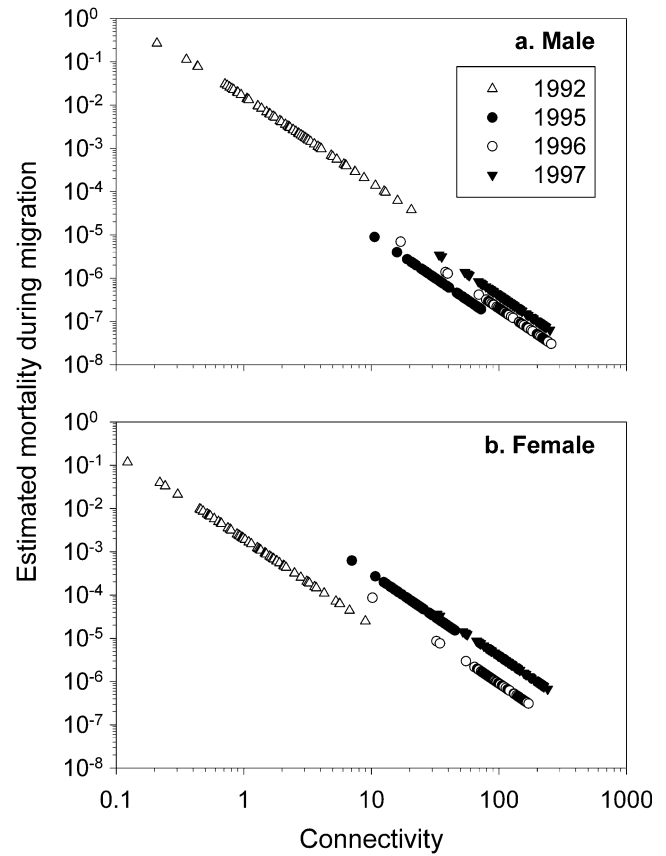


Fig. 5 Estimated mortality during migration for **a** male and **b** female *T. tetraophthalmus* per migration event from each patch plotted versus patch connectivity. Data shown are from 1992 (open triangle), 1995 (filled circle), 1996 (open circle) and 1997 (inverted filled triangle). Connectivity was calculated using Eq. 2 and parameter estimates for each sex in each year (see Materials and methods). Mortality during migration for each patch was calculated using Eq. 3. It should be noted that within a year the model assumes that surviving dispersal increases with connectivity; between years all parameters were free to vary, thus mortality during migration could increase, decrease, or remain constant

1996 ($\chi^2 = 253.08$, $df = 87$, $P < 0.001$; $\chi^2 = 206.40$, $df = 87$, $P < 0.001$), and 1997 ($\chi^2 = 134.46$, $df = 97$, $P = 0.007$; $\chi^2 = 191.97$, $df = 97$, $P < 0.001$, for males and females, respectively). When examined on a per patch basis, the significant lack of fit for immigration was largely due to the model misestimating values for particular patches, rather than systematic misestimation. Considering both sexes in all years, 9.5% (61/640) of tests of immigration on a per patch basis showed significant lack of fit.

Discussion

Promoting migration among populations is a strategy that can aid the conservation of certain species, in

certain habitats. Increasing migration among populations should increase metapopulation persistence, decrease inbreeding depression, and potentially reduce demographic stochasticity (Saccheri et al. 1998; Hanski 1999; Hudgens and Haddad 2003). There are also inherent risks in linking populations via migration (Simberloff et al. 1992) or simply increasing migration rates (Lindenmayer and Lacy 1995). Central to successful migration is surviving the processes. This study provides the first direct empirical demonstration that increasing the size and number of patches and decreasing interpatch distance within a landscape increases the amount of migration among patches and enhances the survival of migrating individuals. That mortality during migration increases with increasing interpatch distance had been a valid, but untested, assumption of many models. Within a period over which parameters are estimated, it is even an assumption of the model used here (see Eq. 3). It should be noted that for the present study parameters were fit independently for each sex, each year and were free to vary for each year. Thus, as the landscape changed between years the model structure did not necessitate that migration mortality would decrease.

Several studies have shown that modifying landscapes, particularly through corridors, can promote migration among habitat patches for some species (Bowne et al. 1999; Haddad 1999; Haddad et al. 2003). A nagging question surrounding this line of investigation is the degree to which increases in migration are offset by increasing migration mortality, i.e., how many more emigrants die in producing a successful immigrant (Hudgens and Haddad 2003)? For *T. tetraophthalmus*, there was an increase in the amount of migration and a decrease in migration mortality as the landscape changed. For this system the large decrease in migration mortality mitigated any increase in mortality due the rise in the number of migrants. It should be noted that the changes occurring in this landscape were unlike creating habitat corridors. If migration is risky, the costs in terms of increased migration mortality could outweigh the benefits of increased immigration. Restoration or habitat alteration plans that will increase migration, especially in potentially hazardous areas, need to account for the costs associated with increased migration (Ries et al. 2001).

The observed decrease in the probability of mortality occurring during migration was profound for this system, but the overall impact of the increase in survival was relatively minimal, except for the most isolated patches in this system. The small overall effect is due to the low amount of mortality occurring during

migration prior to changes in the landscape. Low migration mortality would be expected for this species as these beetles are subject to minimal vertebrate predation (Farrell 2001) and migration distances are short. Comparable increases in the survival of migrants in other systems to that seen here could substantially increase population persistence, particularly where mortality during migration is high or colonization processes are important.

Although the results of this study are in agreement with the theoretical expectations that decreasing interpatch distance and increasing patch number and size reduces migration mortality, they do need to be tempered. First, the results are wholly observational and correlative. Any number of uncontrolled for and unaccounted for factors could possibly be responsible for the observed decrease in migration mortality. I also note that there was not a systematic decrease with each year of systematically decreasing isolation. There was a large decrease in mortality from 1992 to 1995 concurrent with a large increase in patch number and size over the same time period; however, increasing connectivity from 1995 to 1997 did not always result in lower estimated migration mortality. The lack of a consistent response during this period likely represents natural variation in combination with the low amount of mortality occurring during migration.

A second concern is the lack of fit of the VM model. The poor fits were rather surprising given that the connectivity metric used in the VM model explains a large amount of variation in immigration (18–45%, mean 32%) for the 1995–1997 data (Matter et al. 2005). The lack of fit may arise for several reasons. First the beetles may not be responding exactly as modeled. Although the frequency of dispersal declines with distance for these beetles, a negative exponential dispersal kernel is only a rough approximation, especially for females (Matter 1996). A larger problem concerning the lack of fit involves the manner in which it is estimated. Fit of the VM model is estimated using data collected on consecutive dates (Hanski et al. 2000). Mark–recapture censusing on consecutive dates was only done during the emergence period. Therefore there is a limited amount of somewhat biased data with which to test the model. Finally, other factors such as sex ratio (Lawrence 1987) and flowering of the host plant (Hartman 1977; Matter et al. 1999) can affect the migration of this beetle, but are not included in the model. These factors likely contribute to patch specific cases of lack of fit. The tests of lack of fit should be interpreted somewhat liberally here, as they can only provide a rough estimate of fit.

Despite its limitations, this study provides the first empirical evidence that increasing the size and number of patches and decreasing interpatch distance will decrease migration mortality. Efforts designed to decrease migration mortality need to explicitly examine these factors while keeping in mind that the relative benefits of augmenting patch size or decreasing interpatch distance will depend on the species and the specific landscape (Mennechez et al. 2004; Matter et al. 2005).

Acknowledgements A. Greco, J. Landry and C. LaCourse assisted with the fieldwork. B. Hanke, J. Roland, T. Roslin, the University of Cincinnati's EEB discussion group, and two anonymous reviewers provided valuable comments and criticism. I thank I. Hanski for suggestions and A. Moilanen for augmenting the VM model to handle a large number of patches. This research was supported by NSF grants (DEB-9623127 and 0326957) and the University of Virginia's Blandy Experimental Farm.

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