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The influence of matrix habitat on *Aphthona* flea beetle immigration to leafy spurge patches

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Abstract Variation in movement ability by insects among different non-habitat (matrix) types may have important implications for both metapopulation dynamics and weed biocontrol practices. We used a mark-recapture experiment to explore the effects of two different matrix habitats (grass vs shrub) on the ability of two species of *Aphthona* (Chrysomelidae: Coleoptera) flea beetle to immigrate to patches of the invasive weed, leafy spurge. Using generalized linear models, we compared effects of the matrix habitat types, species and sex on observed immigration probabilities. Our analyses demonstrated that one species (*A. nigriscutis*) had a much higher immigration probability when moving through a grass-dominated matrix than a shrub-dominated matrix whereas immigration probabilities for the second species (*A. lacertosa*) were similar in both matrix habitats but significantly lower overall than for *A. nigriscutis*. Furthermore, *A. nigriscutis* females were more likely to immigrate to spurge patches embedded in a grass matrix than in shrub, whereas the opposite occurred for males. Our results suggest that metapopulation dynamics may be strongly affected by the type(s) of matrix habitat present on a landscape. These effects also suggest that release strategies for weed biocontrol should be tailored according to the structure of the landscape into which releases are planned. In addition, even closely related species can have significantly different movement abilities which will also affect release strategies.

Keywords Biological control · Connectivity · Dispersal · *Euphorbia esula* · Landscape · Non-habitat · Metapopulation

Introduction

Dispersal between local populations has long been recognized as a potentially important influence on local population dynamics and broader-scale population persistence (Andrewartha and Birch 1954; Den Boer 1968; Levins 1970; Brown and Kodric-Brown 1977; Pulliam 1988). Current theory has expanded upon Levins' (1970) original ideas about metapopulation dynamics and placed them in a more spatially explicit framework (e.g., Hanski 1994) so that models now account for the size, spatial arrangement of local populations and the potential 'rescue effect' of immigration prior to population extinction (Hanski 1994, 1998; Stacey et al. 1997). These enhancements have generalized the metapopulation concept so that many forms of population structure are now recognized (Harrison and Taylor 1997). However, difficulties remain in exploring how both population structure and landscapes influence population dynamics (Kareiva 1990), primarily because dispersal is a difficult process to measure and model, especially on complex landscapes (Kareiva and Wennergren 1995; Wiens 1997).

Landscape ecologists define landscape spatial structure as the composition and spatial configuration of habitats on a landscape (Dunning et al. 1992; Taylor et al. 1993). An important question addressed is "How does landscape spatial structure influence animal dispersal?" Recent studies in this field demonstrate that components of landscape spatial structure such as patch size, patch aggregation and amount of suitable habitat influence the ability of animals to disperse over landscapes (e.g., Wiens et al. 1997; Pither and Taylor 1998; McIntyre and Wiens 1999; Jonsen and Taylor 2000). However, less attention has been paid to the effect of unsuitable habitat (hereafter referred to as matrix habitat) on animal movement (but see Kareiva 1985; Åberg et al. 1995; Roland et al. 2000 for examples).

The type(s) of matrix habitat present in a landscape and their spatial configuration are features that can potentially influence an animal's ability to disperse suc-

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cessfully among patches of suitable habitat (e.g., breeding habitat). Matrix habitat may confer a high mortality risk (St. Clair et al. 1999; Zollner and Lima 1999; Hanski et al. 2000), physically impede movement (e.g., Crist et al. 1992; Johnson et al. 1992), have some marginal value as a resource (Fahrig and Merriam 1994; Wiegand et al. 1999), or may even facilitate movement (e.g., Matthysen et al. 1995; Taylor and Merriam 1995; Pither and Taylor 1998). The first three factors may reduce or completely prohibit movement across landscapes (landscape connectivity; sensu Taylor et al. 1993), while the latter obviously increases landscape connectivity. Changes in landscape connectivity can influence immigration or colonization probabilities (e.g., Gustafson and Gardner 1996) and thus influence metapopulation dynamics.

We explore some of these ideas in the context of a weed biocontrol system comprising an invasive weed, leafy spurge (*Euphorbia esula* L.), and two introduced flea beetle species (Chrysomelidae: Coleoptera), *Aphthona lacertosa* (Rosch) and *A. nigriscutis* Foudras. The practice of biological control has benefited from recent modelling studies (e.g., Rees and Paynter 1997) that seek to identify the vulnerable stages of targeted weeds and predict the effects of various biocontrol strategies (McEvoy and Coombs 1999). However, more studies are required that can generate useful guidelines for practitioners (Shea and Possingham 2000). Because weed biocontrol is conducted on heterogeneous landscapes, we suggest that using a landscape ecology approach to studying population processes will generate new insight into some of the underlying features responsible for successful biocontrol.

An important goal of weed biocontrol is to create and sustain outbreaks of the control agent on the target weed. The spatial scale at which these outbreaks are achieved and the method used may be influenced strongly by interactions between the control agent's dispersal ability/behavior and landscape spatial structure. For example, the number of releases required to achieve an outbreak and the scale at which those releases are distributed may, in part, be dictated by the dispersal ability of the biocontrol insect, the degree of isolation among weed patches, and the type(s) of intervening matrix habitat.

Here we compare the influence of two types of matrix habitat (grass vs shrub) on the ability of *A. lacertosa* and *A. nigriscutis* to immigrate to isolated patches of their host plant, leafy spurge. Little is known about the dispersal abilities of the two species, but the species are reported to differ in their fine-scale habitat preferences. In its native range, *A. lacertosa* is commonly found in moist areas often containing dense leafy spurge or other vegetation (Gassmann 1990). In North America, *A. nigriscutis* establishes best in open, dry areas with low-density leafy spurge (Maw 1981; McClay et al. 1995). In our study region (S. Alberta, Canada), we also have found *A. nigriscutis* adults on dense spurge patches and on patches embedded in shrubs (I. Jonsen, personal observation). In light of these differences in fine-scale hab-

itat preference, we are interested in determining whether or not the two beetle species have different immigration abilities on the two landscape types. We use a mark-recapture experiment to directly assess how immigration ability differs between species and between sexes on landscapes dominated by either grass or shrub matrix habitat.

Materials and methods

Study system

Leafy spurge is an introduced, perennial weed that invades uncultivated land. It is native to Eurasia but is found throughout most of Canada and Northern United States (Best et al. 1980; Watson 1985). However, its greatest impact as a pest species occurs on rangeland in the Great Plains states and the Prairie provinces (Watson 1985). New infestations are established from dispersed or dormant seeds and have a distinct spatial patchiness which can gradually coalesce into large, continuous stands via clonal spreading. These large stands potentially displace native rangeland plant species and also eliminate productive grazing land because leafy spurge is toxic to cattle.

Five species of flea beetle in the genus *Aphthona* have been released in Canada and the United States since 1982 (McClay et al. 1995) in an attempt to control leafy spurge. To date, the two most successful of these insects, in terms of increased population densities and impact, are *A. nigriscutis* and *A. lacertosa*. The other three *Aphthona* species (*A. flava*, *A. cyparissiae*, and *A. czwalinae*) are much less common in our study area. Both *A. nigriscutis* and *A. lacertosa* are univoltine in Canada (Maw 1981; Gassmann 1990), adults emerge in mid- to late June and feed on leafy spurge foliage. Females lay eggs in the soil near leafy spurge stems and after eclosion the larvae move through the soil and begin feeding on leafy spurge roots. Beetles overwinter as larvae and pupate in mid- to late May.

We conducted beetle releases on ten landscapes, seven located on the Blood Indian Reserve, AB, CAN (49° 23' N, 113° 00' W) and three in the Oldman River valley, Lethbridge, AB CAN (49° 41' N, 112° 50' W). Distances between individual landscapes ranged from 1.3 to 29.6 km. Each landscape consisted of a single leafy spurge patch (the 'target' patch) isolated from other patches by at least 600 m in the general direction of the release transect (see 'Experimental design'). In addition, each target patch was embedded in a landscape of either grass-dominated or shrub-dominated matrix habitat that extended at least 400 m away from the target patch. Each grass landscape consisted of a matrix composed of at least 90% cover of native and introduced grass species. All grass landscapes were heavily grazed by cattle and so contained no shrub cover. Each shrub landscape had a matrix composed of between 60% and 75% cover of shrubs (predominantly *Salix* spp.) ranging from 1 to 2 m in height. The remaining 25–40% of the matrix was composed of grass and bare ground; however, in all cases the release points and the target patches were embedded in shrub habitat. We selected target leafy spurge patches that were approximately equal in size (grass: 40.58±14.47 m², shrub: 44.83±9.86 m²; mean ± SD) to eliminate a potential confounding interaction between patch size and matrix habitat.

Experimental design

All releases were initiated within the period 14–24 July 1999. *A. nigriscutis* and *A. lacertosa* were collected from three 'nursery' sites on the Blood Indian Reserve, the latter species was also collected from the Stoney Indian Reserve, AB, CAN (51° 09' N, 114° 50' W). The releases were designed to compare the influence of two kinds of matrix habitat (grass vs shrub) on the ability of both species to immigrate to isolated leafy spurge patches.

Beetles collected from nursery sites were stored overnight in a rearing cage at 10°C and provided with freshly clipped leafy spurge stems. Approximately 5–6 h prior to release, beetles were marked with fluorescent powder in groups of between 400 and 450. Beetles were aspirated from the rearing cage and passed into an Erlenmeyer flask containing a tissue liberally dusted with fluorescent powder. Once marked, beetles were aspirated individually into a 250-ml plastic Nalgene bottle with a mesh lid. This second aspiration allowed us to (1) count the actual number of beetles allotted for each release and (2) to reject individuals that were marked with too much or too little powder (as per Kareiva 1982).

All releases were conducted approximately 1 h after the last group of beetles was marked (i.e., at ca. 1600–1700 h). Each of the ten landscapes consisted of a single target leafy spurge patch into which both beetle species were released in groups of between 400 and 450 (the exact number was noted for each release). These releases in the centre of target patches (0 m) provided expected recapture proportions for each target patch. In addition we also released between 400 and 450 individuals of both species at 100 and 200 m along a transect away from each target patch. These two releases were situated in either grass-dominated or shrub-dominated matrix habitat. The orientation of the release transects relative to the target patches differed among landscapes because we had to ensure that no other leafy spurge patches were closer than the target patch to the 100 and 200 m release points. Initial analyses indicated that release orientation had no significant effect on results and therefore was ignored.

Different colors of fluorescent powder were used to distinguish beetles from each release point (0, 100 and 200 m) on a single landscape. Releases conducted in a grass and a shrub landscape were paired by release date. This approach ensured that releases in grass and shrub landscapes experienced approximately the same initial weather conditions.

After releases, target patches were sampled every 2–3 days over a 2-week period. Patches were sampled systematically with a sweep net by walking through the patch along parallel lines spaced approximately 1 m (i.e., one sweep net arc) apart. In the field, sweep net contents were carefully extracted into 1-l plastic containers and subsequently placed into a freezer to kill all insect fauna. *Aphthona* beetles were separated from other fauna, inspected for powder marks and sexed under a dissecting microscope at 40× magnification using both UV and fibre-optic light sources. During initial processing we determined that the fibre-optic light source was adequate to locate even minute powder marks on beetles and so this method was used thereafter. Individual beetles were scored as marked or unmarked and the color of powder – indicating release location – was noted.

Most target patches were occupied by *A. nigriscutis* prior to releases but no patches were occupied by *A. lacertosa*. Occupancy of *A. nigriscutis* prior to releases may have influenced the patch occupancy (immigration to or emigration from) of experimentally released beetles. However, this is unlikely to be important in the context of the experimental design because recaptures of matrix habitat-released individuals were compared only to recaptures of controls and not to recaptures of unmarked beetles. Our estimates of immigration ability are likely to be conservative because we cannot detect individuals that successfully immigrate to target patches from a distance and subsequently emigrate or die. We therefore assume that these rates of disappearance are similar to those of our control individuals (i.e., individuals released at 0 m, inside target leafy spurge patches).

Statistical analyses

Recapture data were analyzed using quasi-likelihood regression (McCullagh and Nelder 1989) with proportion recaptured as the response variable and SPECIES, LANDSCAPE, and RELEASE LOCATION as predictors. (Factors included in statistical models are presented in small capitals.) We used quasi-likelihood regression because our data were highly under-dispersed. Unlike some other generalized linear models (i.e., Poisson or binomial) which assume a dis-

persion equal to one, quasi-likelihood models use a dispersion parameter estimated from the data and therefore produce more reliable parameter estimates and significance levels. Because recapture rates were low, data were pooled among the two matrix habitat release distances (100 and 200 m), thus RELEASE LOCATION indicates whether beetles were released in target patches (controls) or in the matrix habitat (grass or shrub). Initial analyses indicated that recaptures of 200-m released beetles were significantly lower (both species) than for those released at 100 m ($F_{1,79} = 7.04$, $P < 0.01$), as might be expected. But there were no interactions between SPECIES or LANDSCAPE and RELEASE DISTANCE from the target patch (RELEASE DISTANCE × SPECIES: $F_{1,79} = 0.08$, $P = 0.79$; RELEASE DISTANCE × LANDSCAPE: $F_{1,79} = 0.03$, $P = 0.86$; RELEASE DISTANCE × SPECIES × LANDSCAPE: $F_{1,79} = 0.93$, $P = 0.34$). Therefore, pooling data among the 100 and 200 m release points increased overall recapture rates without significantly altering or obscuring the relationships of primary interest between immigration ability and SPECIES, LANDSCAPE, or RELEASE LOCATION (releases in the target patch vs releases in the surrounding matrix).

Recaptures from individual sample days were pooled over the entire 2-week sampling period to eliminate any effect of time on recapture distributions. Differences in sampling effort among target patches were controlled statistically by fitting the covariate SWEEPS in all models before assessing effects of design factors. SWEEPS is the total number of sweep net arcs in each patch over the 2-week sampling period. For all analyses, full models (main effects plus all interactions) were fit, including the covariate SWEEPS as the first term of each model. Because the terms of interest are the interactions with the RELEASE LOCATION factor we present only these terms in ‘analysis of deviance’ tables. Analysis of deviance tables are analogous to ANOVA tables, except that the variance component reported is the deviance rather than the sums of squares (see McCullagh and Nelder 1989 for a full discussion of deviance and generalized linear models).

Subsequent analyses were conducted using SEX as an additional predictor. Due to the design of the experiment it was impossible to sex all individuals prior to release. We therefore estimated sex ratios by dissecting a sub-sample of both species of beetle used in each release (*A. lacertosa* $n = 324$, *A. nigriscutis* $n = 302$). These ratios were applied to the numbers of beetle released in each replicate as an estimate of the numbers of male and female beetles released. Subsequent recaptures were separated by sex and recapture proportions were determined for each sex. For this analysis, we fit separate quasi-likelihood models for each species. The response variables are proportion recaptured and the predictors are: SEX, LANDSCAPE, and RELEASE LOCATION.

In order to visualize the nature of significant interactions, we present interaction plots using the mean *relative* proportion of beetles recaptured as the response variable. This measure, although different from the response used in the statistical models, allows us to summarize the important interactions between SPECIES, LANDSCAPE and RELEASE LOCATION in a single graph. The effect of RELEASE LOCATION (beetles released in either target patch or in matrix) is incorporated into the response by dividing the proportion of recaptured beetles released in the matrix by the expected recapture proportion (i.e., the proportion of recaptured beetles released in the target patch).

Due to the relatively broad-scale nature of this experiment, we maximized the numbers of beetles released to ensure sufficient recaptures. By focusing on maximizing recaptures and with a limited number of beetles available, we were able to replicate our landscape treatment 5 times (5 of each matrix habitat type). Based on this replication, we a priori set an alpha level of 0.1 for all statistical models.

Results

A total of 25,956 beetles was released over all ten landscapes. Table 1 presents a summary of the numbers of beetle released and recaptured according to each design

Table 1 Number of beetles released and recaptured (in parentheses) in target leafy spurge patches according to the design factors: RELEASE LOCATION, SEX, SPECIES and LANDSCAPE. Estimated, prior-to-release sex ratios (see Materials and methods) are provided under the species column

SPECIES	RELEASE LOCATION	LANDSCAPE			
		Grass		Shrub	
		Male	Female	Male	Female
<i>A. nigriscutis</i> 0.0201 Male; 0.9799 Female	Target patch	43 (7)	2114 (238)	45 (7)	2199 (162)
	Matrix	85 (2)	4120 (89)	93 (1)	4556 (3)
<i>A. lacertosa</i> 0.4969 Male; 0.5031 Female	Target patch	1184 (75)	1198 (68)	1072 (47)	1085 (70)
	Matrix	1853 (6)	1876 (8)	2203 (1)	2230 (4)

Table 2 Analysis of deviance table. The response variable is the proportion of *Aphthona lacertosa* and *A. nigriscutis* recaptured in target leafy spurge patches. Beetles were marked, released and recaptured on either grass or shrub landscapes. The model is a Quasi-likelihood model fit with binomial errors. Full models (main effects plus all interactions) were fit but only terms including the release location factor are presented (see Materials and methods)

Term	df	Deviance	F-value	P(F)
Null	39	2.011		
RELEASE LOCATION	1	0.007	141.541	<0.001
RELEASE LOCATION × SPECIES	1	0.006	0.705	0.408
RELEASE LOCATION × LANDSCAPE	1	0.067	7.463	0.010
RELEASE LOCATION × SPECIES × LANDSCAPE	1	0.070	3.918	0.030
Residual	31	0.289		

Table 3 Analysis of deviance table. The response variable is the proportion of male and female *Aphthona lacertosa* recaptured in target leafy spurge patches. Beetles were marked, released and recaptured on either grass or shrub landscapes. The model is a Quasi-likelihood model fit with binomial errors. Full models (main effects plus all interactions) were fit but only terms including the release factor are presented (see Materials and methods)

Term	df	Deviance	F-value	P(F)
Null	39	2.237		
RELEASE LOCATION	1	1.208	34.928	<0.001
RELEASE LOCATION × SEX	1	0.001	0.021	0.885
RELEASE LOCATION × LANDSCAPE	1	0.006	0.181	0.674
RELEASE LOCATION × SEX × LANDSCAPE	1	0.020	0.283	0.756
Residual	31	0.945		

factor. Overall recapture rates were very low (3%) but sufficient to detect effects of experimental treatments.

A. lacertosa had similarly low abilities to immigrate to patches of leafy spurge embedded in both grass- and shrub-dominated LANDSCAPES, while *A. nigriscutis* was more likely to immigrate to spurge patches on grass-dominated landscapes than on shrub-dominated ones (Table 2, significant RELEASE LOCATION × SPECIES × LANDSCAPE INTERACTION; Fig. 1). Ignoring landscape type (shrub vs grass), there was also an overall difference in immigration ability between *A. lacertosa* and *A. nigriscutis* (Table 2, significant release location × species interaction), suggesting that *A. nigriscutis* is a better overall colonizer of leafy spurge patches than is *A. lacertosa* (Fig. 1).

Table 4 Analysis of deviance table. The response variable is the proportion of male and female *Aphthona nigriscutis* recaptured in target leafy spurge patches. Beetles were marked, released and recaptured on either grass or shrub landscapes. The model is a Quasi-likelihood model fit with binomial errors. Full models (main effects plus all interactions) were fit but only terms including the release location factor are presented (see Materials and methods)

Term	df	Deviance	F-value	P(F)
Null	39	5.517		
RELEASE LOCATION	1	3.228	64.714	<0.001
RELEASE LOCATION × SEX	1	0.018	0.359	0.553
RELEASE LOCATION × LANDSCAPE	1	0.010	0.192	0.664
RELEASE LOCATION × SEX × LANDSCAPE	1	0.322	3.230	0.053
Residual	31	1.646		

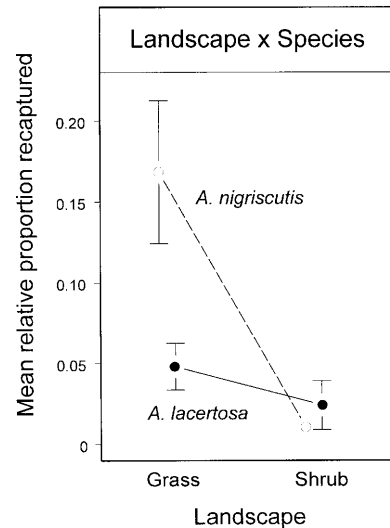


Fig. 1 Interaction plot of the mean relative proportion of beetles recaptured in target leafy spurge patches embedded in grass and shrub landscapes, according to species. This response incorporates the effect of release location by scaling recapture proportions of matrix-released beetles by the expected recapture proportions (beetles released and recaptured in target patches). Lines indicate direction of trend between means for each combination of the factors landscape and species. Error bars are ± 1 SE. Pairs of data points in a landscape type are staggered for clarity

Separate analyses of the effects of sex (based on estimated sex ratios, see Materials and methods) and LANDSCAPE on immigration probability indicate that *A. lacertosa* males and females had equally low immi-

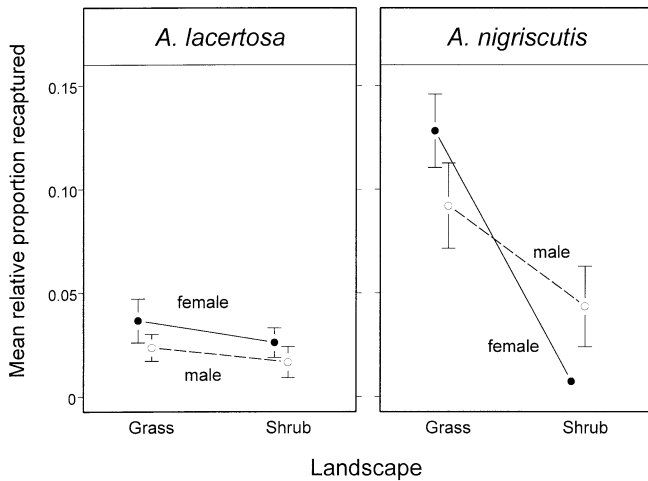


Fig. 2 Interaction plot of the mean relative proportion of *Aphthona lacertosa* and *A. nigriscutis* beetles recaptured in target leafy spurge patches embedded in grass and shrub landscapes, according to sex. This response incorporates the effect of release location by scaling recapture proportions of matrix-released beetles by the expected recapture proportions (beetles released and recaptured in target patches). Lines indicate direction of trend between means for each combination of the factors landscape and sex. Error bars are ± 1 SE. Pairs of data points in a landscape type are staggered for clarity

gration ability on grass- and shrub-dominated landscapes (Table 3, no significant interactions between RELEASE LOCATION, SEX, or LANDSCAPE; Fig. 2). However, *A. nigriscutis* females had a higher immigration ability than males on grass-dominated LANDSCAPES, whereas males had a higher immigration ability on shrub-dominated LANDSCAPES (Table 4, significant release LOCATION \times SEX \times LANDSCAPE interaction; Fig. 2).

Discussion

Our experimental design enabled us to assess the connectivity (Taylor et al. 1993), here measured as immigration probability, of the dominant (grass) and a less common (shrub) landscape encountered by *Aphthona* beetles released in our study region. We show here that the type of matrix habitat surrounding host patches has a strong influence on the immigration ability of *A. nigriscutis*, while for *A. lacertosa* immigration ability is similar between the two landscape types. We assume released beetles either locate leafy spurge patches embedded in the grass or shrub matrix habitat or perish because both species are specialists on *Euphorbia* spp. (Gassmann 1990; Gassmann et al. 1997).

Other studies have demonstrated that the surrounding landscape can influence animal movement behaviors. For example, Jonsen and Taylor (2000), focusing at a similar scale to the current study, showed that Calopterygid damselflies readily move away from streams on completely and partially forested landscapes but not on unforested ones. At a much finer scale (i.e., 2–8 m),

Kareiva (1985) found a striking difference in host finding ability of two *Phyllotreta* flea beetles between releases conducted in cultivated ground versus goldenrod matrix habitats. While there were no marked differences between the two *Phyllotreta* species, Kareiva's results parallel those presented here for *A. nigriscutis* in that immigration ability was reduced by the taller and structurally more complex matrix habitat (i.e., goldenrod / shrubs versus cultivated ground / grass). At a broader scale (i.e., 1–4 km), Åberg et al. (1995) demonstrated that habitat isolation effects for the hazel grouse (*Bonasa bonasia*) were much stronger on a landscape dominated by an agricultural matrix than on one dominated by a logged forest matrix. They suggested that the hazel grouse were reluctant to move across the agricultural matrix but readily moved through the forest matrix. Roland et al. (2000) showed a strong negative effect of distance through forest on between-meadow movements of the alpine butterfly *Parnassius smintheus*. This negative effect appears to be due both to a reluctance to enter forest and to reduced rates of movement through forest.

A drawback of mark-recapture experiments such as ours are that they do not allow researchers to determine the behaviors the animals engage in during their travel. Consequently, we are unable to determine the specific mechanism(s) underlying the differential responses of the two *Aphthona* species to the grass versus shrub landscape comparison. Nevertheless, our approach has identified that a difference in immigration ability exists between the two types of matrix habitat studied and between the two flea beetle species. We suspect that the overall difference in immigration ability between the two species may be due a difference in wing size. Despite similar body sizes, *A. nigriscutis* has significantly longer and wider wings than *A. lacertosa* (I. Jonsen, unpublished data). These morphological differences are consistent with our results here, suggesting that *A. nigriscutis* is more capable of traversing the 100- to 200-m distances imposed upon beetles in this study. The morphological difference between species does not, however, explain the effect of matrix habitat on immigration. *A. nigriscutis* prefers open and/or grassy spurge patches (Maw 1981; McClay et al. 1995) and moves well through grass-dominated landscapes, whereas shrub-dominated landscapes may represent behavioral or physical barriers to its movement (e.g., Crist et al. 1992; Johnson et al. 1992). In contrast, *A. lacertosa* prefers mesic, shrubby spurge patches (Gassmann 1990) but has equally low immigration rates in both grass- and shrub-dominated landscapes. Regardless of the specific mechanisms involved, an important next step is to determine whether these differences in movement ability, behavior and/or morphology translate into population-level effects such as lower beetle population incidence on leafy spurge patches embedded in shrub-dominated landscapes.

Our initial observations of post-release distributions of *A. lacertosa* and *A. nigriscutis* on the Blood Reserve indicated that *A. nigriscutis* was much more widely dis-

tributed on leafy spurge patches, up to ca. 700 m from known release sites, than was *A. lacertosa* (I. Jonsen, unpublished data). This is not surprising since, although both species were first widely released in 1997, some localized releases of *A. nigriscutis* were conducted throughout our study region over the past 18 years (McClay et al. 1995). Nevertheless, our results here indicate that the higher connectivity of grass landscapes for *A. nigriscutis* than for *A. lacertosa* may also contribute to the observed distribution patterns. Because shortgrass rangeland is the dominant matrix habitat type with shrubs comprising a smaller proportion in our study region, we would expect that a between-species difference in movement ability through grass matrix habitat (Fig. 1) would have a stronger effect on broader-scale distribution than any difference in movement through shrub matrix habitat.

The significant interaction between sex and landscape type (Fig. 2) for *A. nigriscutis* indicates that females had a larger decrease in immigration ability between grass and shrub landscapes than did males. This difference may reflect oviposition choices made by habitat-seeking females; *A. nigriscutis* prefers open leafy spurge patches in dry, grassy areas over patches in mesic-moist, shrubby areas (Maw 1981; McClay et al. 1995). Because only mated females can found new local populations, this interaction between sex and landscape may have important consequences for local demography of *A. nigriscutis* on shrub-dominated landscapes where females have a lower immigration ability.

Our experimental design imposed distances of 100 and 200 m over which beetles had to travel in order to immigrate to host plant patches. In our study region inter-patch distances range from tens to many hundreds of meters in both grass- and shrub-dominated habitats. In general, our experimental release distances are not unrealistic of the typical inter-patch distances that beetles may encounter when dispersing from one leafy spurge patch to another. Thus we expect that the experimental results presented here are relevant to the population dynamics of both beetle species in our study region.

Implications for metapopulation dynamics

Differences in overall immigration ability between species and between landscapes have potentially important implications for their population dynamics. Current metapopulation theory suggests that enhanced colonization/immigration can increase the persistence of spatially structured populations (Brown and Kodric-Brown 1977; Hanski 1994, 1998). However, too much dispersal among local populations tends to synchronize local dynamics and thus increase the risk of metapopulation extinction (Hastings and Harrison 1994; Gyllenberg et al. 1997). Immigration effects on metapopulation dynamics have been demonstrated in various empirical systems (e.g., Holyoak and Lawler 1996; Stacey et al. 1997); however, relatively little is known about the influence of

landscape spatial structure, especially the composition of matrix habitat, on immigration rates (Gustafson and Gardner 1996; Wiens 1997). Our experimental results indicate that the type of matrix habitat encountered by dispersing individuals can have a profound effect on immigration rates but that these effects may not be consistent among similar species or even between sexes. Roland et al. (2000) found a strong effect of distance through forest matrix habitat on between-meadow movements of *P. smintheus* and suggested that such matrix habitat effects on metapopulation dynamics may be magnified when movement is restricted to linear arrangements of suitable habitat and matrix habitat (e.g., mountain ridge tops or riparian habitat). In contrast, Moilanen and Hanski (1998) found little evidence to suggest that landscape spatial structure influenced the metapopulation dynamics of the butterfly *Melitaea cinxia*. However, their study landscape was relatively homogeneous; increased landscape heterogeneity may also contribute to stronger landscape effects on metapopulation dynamics.

Implications for weed biocontrol

Our results have implications for weed biocontrol in general and for the leafy spurge – *Aphthona* system, in particular. Much of weed biocontrol is conducted on heterogeneous landscapes that are mosaics of weed patches, native and non-native (i.e., crop land) habitats. Once biocontrol agents are established at initial release sites, biocontrol practitioners are interested in the impact of the agent on target weeds, dispersal rates of the agent and the ability of the agent to colonize weed patches some distance from initial release points (e.g., Rees 1990; Mays and Kok 1996; Grevstad and Herzig 1997; McFadyen 1998). Our results indicate that immigration / colonization of weed patches is dependent upon the type of matrix habitat separating source and destination weed patches. This effect appears to vary between closely related species and between sexes. An important consequence for weed biocontrol is that different release strategies may be required depending on the type of landscape encountered and the biocontrol agent used. Based on this study, we predict that on grass-dominated landscapes, *A. nigriscutis* will be better able to colonize and have impact on spurge patches some distance from initial release locations than *A. lacertosa*, at least at a scale of 100–200 m. On shrub-dominated landscapes, however, both species have low colonization abilities and successful biocontrol may only occur when individual releases are conducted at a finer-scale than on grass-dominated landscapes. We are currently exploring these ideas on a large network of leafy spurge patches to determine the extent to which landscape mediated immigration influences within-patch demography of *Aphthona* beetles and, in turn, impact on leafy spurge.

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