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ABSTRACT -- Small patches in fragmented habitats might function as sinks, as islands suitable for colonization, or they might facilitate movement of animals through the matrix from one suitable patch to another even though they might not support self-sustaining populations. Using mark-recapture procedures with the monophagous dogbane beetle (*Chrysochus auratus*), we examined the use of experimental clusters of its host plant, Indian hemp dogbane (*Apocynum cannabinum*), radiating out from large, natural patches. Experimental clusters of plants were placed as single clusters at varying distances up to 100 m from seven natural patches and in "stepping stone" fashion of clusters every 25 m. Based on known movement patterns in the dogbane beetle, we expected that clusters of host plants would be found easily by individuals dispersing from the adjacent natural patch. As expected, over 90% of the experimental host plant clusters were discovered over the course of the season, but the dogbane beetles visiting the clusters of host plants we added were likely long-distance dispersers (> 350 m), given that we found no marked dogbane beetles from the natural patch in any of the plant clusters. We found no effect of the stepping stone arrangement on the number of dogbane beetles captured in the clusters. Furthermore, dogbane beetles only visited the host plant clusters for a short time, presumably to feed and rest, rather than taking up residence and laying egg masses as they did on host plants in natural patches. Preliminary evidence supported the hypothesis that patches of *A. cannabinum* might serve as stepping stones for dogbane beetles moving among large populations of the host plant. For dogbane beetles and other prairie insects dependent on plants found in scattered remnants, small, frequently unoccupied patches might facilitate movement between large patches even though they might not support viable populations.

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Small habitat patches in fragmented landscapes might function in a variety of ways.   They might serve as islands suitable for colonization in mainland-island configurations (Hanski and Gyllenberg 1993), they might function as sinks (Pulliam 1988) and pseudosinks (Watkinson and Sutherland 1995), or they might promote movement of organisms by serving as "stepping stones" between high quality patches in a manner similar to that of corridors (Soulé and Gilpin 1991, Sutcliff and Thomas 1996).   In the tallgrass prairie ecosystem, habitat destruction and fragmentation has caused an increase in small populations in two ways.   First, fragmentation has resulted in reduced population sizes of many native plants sensitive to human disturbance and these small populations now are separated more widely than 150 years ago (Samson and Knopf 1994).   Second, and less frequently, a few native plant species with weedy characteristics have become more abundant in the landscape as small, ephemeral populations because of their ability to occupy disturbed sites created by human activities.   One such plant, Indian hemp dogbane (*Apocynum cannabinum* Apocynaceae), previously was found on prairies and along waterways, but is now much more widespread as a result of its ability to colonize disturbed sites.

For monophagous insects using host plants such as Indian hemp dogbane, small patches might not support breeding populations but might provide temporary food resources, shelter, mating opportunities or function as a refuge from predators (St. Pierre and Hendrix 2003).   Ecologically, dispersal to such patches can be influenced by abiotic conditions, conspecific density, or competition for food, space, or mates.   In general, dispersal between habitat patches is correlated negatively with distance between pairs (Haddad 1999, Hanski 2001) and differences in the size (McIntyre and Wiens 1999) or quality (Boughton 1999) of the patches might influence the magnitude or direction of exchange between them.

In our study, we addressed the use of artificial patches of Indian hemp dogbane by the monophagous dogbane beetle (*Chrysochus auratus* Fabricius) (Coleoptera: Chrysomelidae).   In contrast to the study of Williams (1992) in Virginia that showed dogbane beetles to be infrequent dispersers and patchily distributed among suitable host patches, our preliminary study of this plant-herbivore system in Iowa (St. Pierre et al. 2005) showed that naturally occurring patches with as few as 14 ramets (stems) consistently harbor dogbane beetles and given that the species can disperse up to 4 km between patches, new patches likely are encountered readily.   To test the ability of the dogbane beetle to find and colonize host plant patches, we used experimental clusters of its host plant radiating out from the edges of natural patches to address the following questions: 1) Do

dispersing dogbane beetles find and colonize host plant clusters or just visit them? 2) Are colonizers predominantly from the associated natural patch, as predicted by dispersal distributions for this species (St. Pierre et al. 2005)? 3) Is dispersal to a distant host plant cluster enhanced by the presence of an island chain of plant clusters between it and the natural host plant patch? and 4) Is timing of dispersal influenced by proximal factors such as dogbane beetle density?

METHODS

The dogbane beetle is a monophagous herbivore of dogbanes (*Apocynum* spp.; Apocynaceae) (Weiss and West 1921). Adults are approximately 1 cm long and are brilliant metallic green. The species is found throughout the contiguous United States east of the Rocky Mountains (Peterson et al. 2001). In Iowa, adults are found feeding on the leaf margins of the host plant from mid-June to mid-August. Mating occurs on the plants throughout the summer and females oviposit in a cone of excrement on the stem or the undersides of leaves. Upon hatching, the larvae drop to the ground and tunnel to the roots of the host plant where they feed and overwinter (Williams 1988).

The host plant, Indian hemp dogbane is a native perennial rhizomatous herb found along roadsides, in oldfields, and near waterways throughout most of the contiguous United States except the arid Southwest (Hartman 1986). Spreading dogbane (*A. androsaemifolium*) is another suitable host of the dogbane beetle but we found no populations of it in our study area. Although the dogbane beetle has been reported to be an herbivore of milkweeds (Asclepiadaceae) (Weiss and West 1921), we never observed them feeding on any milkweed species. In a food choice experiment, the dogbane beetle did not feed on milkweed leaf tissue, even when given no other choice (Dobler and Farrell 1999).

Seven sites, each containing a patch of Indian hemp dogbane, were located in Johnson County, Iowa (Table 1). Sites were either prairie remnants supporting diverse plant communities or non-remnants such as oldfields or disturbed roadsides dominated by exotics and few, if any, other native forbs. Remnants did not differ significantly from non-remnants in preliminary analyses of capture frequencies, patch tenure times or dogbane beetle densities and, consequently, both categories were combined in all analyses we report. We counted ramets at all sites.

Adjacent to each of seven natural patches of Indian hemp dogbane we planted 12 clusters of five host plants along six transects arranged at 60° intervals and radiating out from the edge of the patch (Fig. 1). Along four transects, we planted one cluster of five Indian hemp dogbane ramets at one of the four distance categories (25, 50, 75, or 100 m) from the edge of the host patch. We chose these distances because previous mark-recapture studies of the dogbane beetle (St.

Table 1. Study sites in Johnson County, Iowa, their characteristics, the number of dogbane beetles marked in the Indian hemp dogbane patches, and the number of beetles captured in the experimental clusters of Indian Hemp dogbane.

Site	Number of host ramets	Patch area (m^2)	Habitat Type	Number of beetles marked in natural patches	Number of beetles captured in clusters
Hawkeye 2	1233	468	Nonremnant[1]	2230	8
Hoover Trail	1012	2580	Remnant prairie[2]	1505	31
Hawkeye 1	702	340	Nonremnant[1]	539	8
Finkbine 2	454	256	Nonremnant[3]	579	23
Fox Radio	253	365	Nonremnant[1]	559	8
Propane Prairie	180	8390	Remnant prairie[2]	191	6
Finkbine 1	28	20	Remnant prairie[2]	62	22

[1] oldfield: open habitat that was used for agriculture or as a hayfield but has been fallow for at least 10 years.
[2] remnant prairie: relict unplowed tallgrass prairie.
[3] roadside: narrow (10 m or less) right-of-way along a road (usually dominated by exotic grasses and forbs).
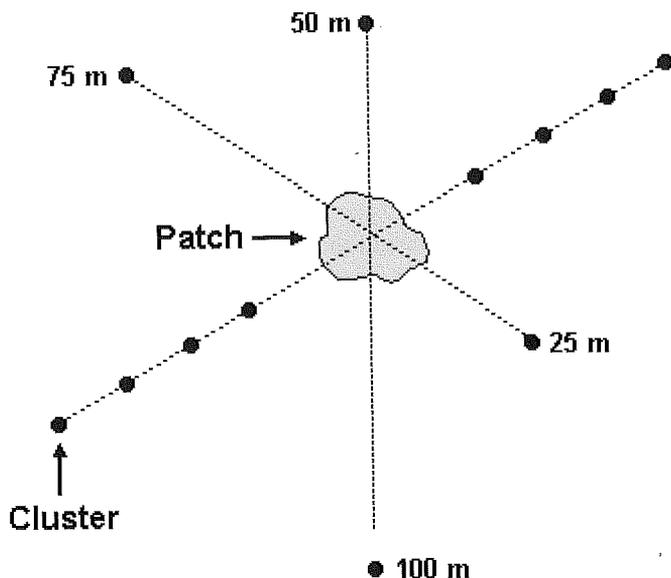
Figure 1. Representative design of experimental clusters radiating from a natural patch. Clusters of five Indian hemp dogbane (*Apocynum cannabinum*) plants were placed at incremental distances from the edge of the host plant patch along transects spaced 60° apart. Islands are represented by single clusters on a transect at varying distances from the edge and stepping stones are represented by the two transects with multiple clusters of Indian hemp dogbane plants.

Pierre et al. 2005) showed that 40% of them moved less than 1 m, 63% less than 10 m, and 94% of the dogbane beetles move less than 100 m between captures (approximately one week). We refer to the four single experimental clusters at varying distances from the natural patch as "island" clusters. Along the remaining two transects, we planted clusters of five Indian hemp dogbane plants at each of the four distance categories. We refer to them as "stepping stone" clusters. Each cluster was approximately 1.0 m² in size. At all seven natural patches, the stepping stone transects were oriented at 180° from each other. We determined which transect received which island cluster based on the availability of open habitat for planting Indian hemp dogbane. All layouts were different from each other with respect to the cardinal directions of the transects.

We reared plants for the experimental clusters from *A. cannabinum* rhizomes collected from an oldfield in Johnson County, Iowa, in late April 2000 when the

shoots were beginning to emerge from the soil. For four weeks the plants grew in 4-liter-sized pots in a greenhouse at the University of Iowa at temperatures of 16 to 27° C. Lighting was not augmented and plants were hardened off over a period of one week before we planted them in the field on May 20, 2000. We watered plants every two days for the first week after planting. At the time of first emergence of dogbane beetles (approximately June 20), the average height of the experimental plants was approximately equal to that of ramets in the natural stands. We did not discern any physical differences (height, vigor, etc.) between the greenhouse-grown Indian hemp dogbane plants and those in the natural patches.

We conducted weekly censuses of the dogbane beetle in the natural Indian hemp dogbane patches and the experimental clusters from mid-June to early August every 6 to 7 days for a total of eight censuses. All censuses were conducted between 0800 CDT and 2000 CDT when dogbane beetles are active and captured easily by hand for marking. Before 0800 and after 2000 hrs dogbane beetles are sluggish and when the host plant is disturbed even slightly they fall to the ground where they are difficult to find. In the natural patches, we labeled dogbane beetles with a patch and date specific mark on their elytra by using different colors of Liquid Paper® correction fluid. With this method, all individuals with the same capture history were marked identically. In a caged trial in an Indian hemp dogbane patch, only one out of 200 beetles lost marks on one elytron and none lost marks on both elytra over a period of two weeks (St. Pierre unpublished data). After marking, we immediately released dogbane beetles on the ground at the base of the host plant. Although many individuals immediately began ascending the host plant, few reached the terminus of any branch and even fewer flew away. For those that did take flight, they invariably flew to an adjacent branch of that host plant or to an adjacent host plant within 2 m. In the experimental clusters, we individually marked dogbane beetles on an elytron with a patch specific color of correction fluid, uniquely numbered them by using a black ultra fine Sharpie® permanent marker, and immediately released them at the base of the host plant in the cluster from which they were captured.

To determine if marked dogbane beetles from the natural patches or experimental clusters were dispersing to host patches beyond our study areas, we visited all *A. cannabinum* patches within a 700 m radius of the clusters and examined the dogbane beetles in these patches for marks. We did not mark any beetles in those patches.

We estimated dogbane beetle population size in the Indian hemp dogbane patches by using the Jolly-Seber method implemented with the program CAPTURE-RECAPTURE (Young and Young 1998). For those sites/censuses that had too few marked or recaptured dogbane beetles for reliable estimation with the Jolly-Seber method, we calculated Lincoln-Petersen estimates of population size (Pollock et al. 1990). We defined patch tenure time as the number of days between the first and last capture of a dogbane beetle within a patch, which made it a minimum estimate.

We analyzed capture frequencies in the experimental clusters of plants by using analysis of covariance (ANCOVA) and by treating patch and census as random effects and transect type (island or stepping stone) and distance as a fixed effect. We eliminated interaction terms in a stepwise fashion from the analyses when they did not contribute significantly ($p > 0.20$) to the model and then reanalyzed the data. We calculated Pearson's product moment correlations to judge the relationship between capture frequency in the clusters and dogbane beetle density or population size in the natural patches at the same census. Because multiple comparisons were made, we adjusted p values for each test to control the overall experimentwise error rate. We also incorporated a one week time lag between dogbane beetle density or population size and capture frequency in the experimental clusters because dogbane beetles typically stay in the natal host patch 7 to 10 days before dispersing (St. Pierre et al. 2005).

RESULTS

From June 25 to August 9, 2000, we marked a total of 5,665 dogbane beetles in the natural patches (Table 1) and we captured 106 dogbane beetles in the experimental clusters surrounding the natural patches. We captured dogbane beetles in 45% of the experimental clusters, but we noted leaf damage characteristic of dogbane beetle feeding (see Williams 1991) in 94% of the clusters. No dogbane beetles marked in the natural patches subsequently were caught in their associated experimental cluster. In the natural patches we recaptured approximately 19% of all marked dogbane beetles at least once and, based on estimates of the population size at each patch, we marked 23.2% (S.E. = 8.86; n = 7) of the dogbane beetles in these patches. In contrast, we recaptured only five (5%) of the 106 dogbane beetles captured in the experimental clusters. Three of these five dogbane beetles had remained in the cluster in which they were first captured, one of them moved 100 m to the natural host patch associated with the experimental cluster, and one of them moved to a natural host patch (350 m away) not examined in our study. The number of dogbane beetles arriving at the experimental clusters did not significantly differ among patches or transect types (island or stepping stones) and was not related to the distance between the cluster and the natural patch (Table 2). Overall, more beetles were captured in island clusters than in the stepping stone clusters for all distance categories except 25 m.

Dogbane beetle density and the total number of dogbane beetles in experimental clusters peaked about a month after they began to emerge and dropped off by early August (Fig. 2). We found a significant relationship between the total number of dogbane beetles captured at the experimental clusters around each of the natural patches at a census and the average dogbane beetle density in all the natural patches in the previous census (n = 7, r = 0.94, p < 0.01), a

Table 2. The effects of patch, transect type (island or stepping stone), and distance from natural host on the number of beetles captured in the experimental clusters are shown by ANCOVA. All other interactions were omitted from this analysis because they were not significant at p = 0.50 in a preliminary analysis. Patch and transect type were treated as discrete variables and distance was treated as a continuous variable.

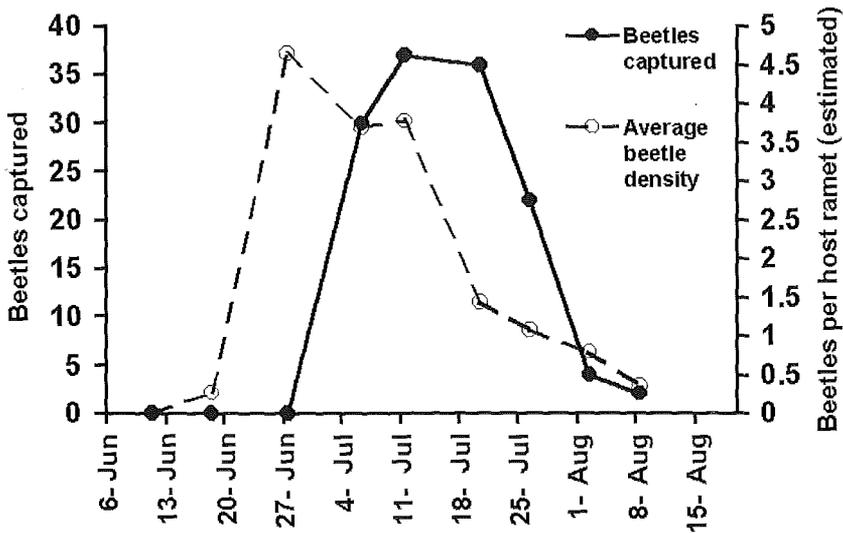| Source	d.f.	Type III SS	MS	F value	Pr > F
Full Model[1]	9	77.74	8.64	1.19	0.33
Patch	6	65.29	10.88	1.50	0.21
Transect	1	0.39	0.39	0.05	0.82
Distance	1	2.89	2.89	0.40	0.53
Error	33	231.92	7.03		

[1]model R^2 = 0.25

Figure 2. Total number of dogbane beetles captured in the experimental clusters at a census and the average dogbane beetle density across all natural Indian hemp dogbane patches (equally weighted) over time.

measurement that accounts for effects of regional levels of dogbane beetle numbers or activity. The total number of dogbane beetles captured at the clusters, however, was unrelated to average dogbane beetle density across all patches at that census (n = 7, r = 0.63, p = 0.13), average $\log_{10}$ dogbane beetle population size in the natural patches at that census (n = 7, r = 0.43, p = 0.34), or average estimated maximum dogbane beetle population in the patches at that census (n = 7, r = 0.42; p = 0.35). We found no relationship between the total number of dogbane beetles arriving at all the experimental clusters around a natural patch and the number of host plants in the natural patch (n = 7, r = 0.10; p = 0.84).

The average tenure time of recaptured dogbane beetles in the natural host patches was 12.5 days (S.E. = 0.5 days), an amount of time comparable to other studies of this species in Johnson County, Iowa (St. Pierre et al. 2005). Although 106 dogbane beetles were captured in the experimental clusters, only three of them were recaptured there and the tenure time for those three individuals was 6 days, the minimum time between censuses.

No deleterious effects of the markings were observed. Marked beetles behaved (in flight, crawling, feeding, mating, and ovipositing) no different from unmarked beetles.

DISCUSSION

Our results indicated that small host plant patches of Indian hemp dogbane such as the ones we created in the experimental clusters were found easily by dogbane beetles, given that we captured dogbane beetles or saw characteristic damage by them in over 90% of the experimental clusters of plants surrounding the seven natural patches. However, two lines of evidence indicated that the individuals locating these clusters were only visiting the clusters for short periods of time and were not founding new populations. First, we recaptured far fewer marked dogbane beetles in the clusters than in natural patches (5 vs. 19%) and the tenure time of the few dogbane beetles recaptured in the experimental clusters was considerably shorter (6.0 days; S.E. = 0 days) than in larger, natural patches (12.5 days, S.E. = 0.5 days). Second, we never found egg masses in the experimental clusters whereas we found as many as 25 egg masses on the stem and leaves (St. Pierre, personal observation) of ramets in the natural patches.

Our data also indirectly indicated that dogbane beetles visiting the experimental clusters were relatively long distance dispersers (> 350 m) rather than local residents from the adjacent natural patch as expected based on studies of dispersal (St. Pierre et al. 2005). We reason this because we marked approximately 23% of the beetles in the natural host plant patches, so 23% or 24 of the 106 dogbane beetles captured in the experimental clusters already should have been marked, if the associated natural patches were the sole

source of these beetles. However, none of the dogbane beetles we caught in experimental clusters had been marked previously in the adjacent natural patch, which suggested that few of the dogbane beetles captured in the clusters were from adjacent natural patches. The dogbane beetles found in the clusters probably were not all recently emerged, unmarked individuals from the associated natural patches because we showed in another study of dogbane beetle (St. Pierre et al. 2005) that marked individuals usually remained at their initial capture location for at least one week before dispersing.

The absence of relationships between transect type (island or stepping stone) or distance (25, 50, 75, or 100 m) and the number of dogbane beetles captured in the clusters is further indirect evidence that the dogbane beetles were coming from more distant sites. Possibly, dispersing individuals do not search actively for host plants until they have flown greater than 100 m (or a time period that results in a displacement of greater than 100 m). Other beetle species such as the striped ambrosia beetle (*Trypodendron lineatum* (Scolytidae)) and the Douglas fir beetle (*Dendroctonus pseudotsugae* (Scolytidae)) require at least 30 minutes of sustained flight before responding to visual or olfactory stimuli from mates or host plants (Bennett and Borden 1971). Because the number of dispersing dogbane beetles arriving at experimental clusters at a census was correlated positively with the average dogbane beetle density in all the natural patches in the previous census, likely the migrants represent surplus individuals leaving natural patches in avoidance of competition for food or mates or perhaps to minimize competition among their offspring for food resources. We hypothesize that small clusters of host plants are used as stepping stones where dogbane beetles rest, feed for a short time, and then disperse again.

If our hypothesis about the use of small clusters of host plants by insect herbivores is correct, many other phytophagous prairie insects could benefit from the creation of small patches that function as stepping stones for dispersal between larger patches. Because establishment of true corridors to increase dispersal is usually not an option for conservation biologists, especially in highly developed landscapes, the creation of small patches that function as stepping stones might be an appropriate alternative that will help prevent some of the negative effects of fragmentation.

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