Two ecologically-divergent generalist predators have different responses to landscape fragmentation

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We conducted three replicated field experiments to test the population response of two ecologically-divergent wolf spider species (*Hogna helluo* and *Pardosa milvina*) to three correlates of landscape fragmentation: area reduction, spatial subdivision, and increased edge to core ratio. We selected these two species because they differ in vagility and habitat selectivity. *Hogna helluo* is relatively large, averse to disturbed substrata, and has poor colonization abilities. Conversely, *Pardosa* is small, vagile, and will use barren, disturbed areas. In a test for the effect of area reduction on populations of the two wolf spiders, we destroyed 0%, 20% or 80% of randomly selected habitat islands in replicated experimental landscapes. We found that population densities of *Hogna* declined significantly, even at the lowest level of area reduction (20%), and that there was an increase in numbers of *Pardosa*. In a test for the response to an increase in landscape subdivision, we created four levels of habitat fragmentation in replicate plots. We found a significant decline in *Hogna* populations with increasing fragmentation. *Pardosa* populations did not respond to the fragmentation. In the third experiment we kept landscape area and subdivision constant, but manipulated the edge-to-core ratio. We found that populations of *Hogna* declined sharply with increasing edge, and that populations of *Pardosa* did not respond. These two syntopic wolf spiders have distinctly different responses to landscape fragmentation.

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Species loss in anthropogenically-fragmented landscapes has been attributed to reduced landscape connectivity, increased patch isolation, reduced population size, and/or the degradation of core habitats through abiotic and biotic edge effects (Meffe and Carroll 1997). Part of the challenge in studying the mechanisms behind the influence of habitat fragmentation on species persistence is that the spatial and ecological attributes of fragmented landscapes have correlated effects (McGarigal and Cushman 2002, Fahrig 2003). For example fragmented landscapes generally suffer a net loss of habitat area in addition to increasing spatial subdivision leading to an overall decrease in connectivity and core habitats (Fahrig 1997, 2002, 2003, McGarigal and Cushman 2002).

Most studies of habitat fragmentation have been correlative studies of the effect of landscape pattern on community richness and diversity (reviewed by Debinski and Holt 2000, Haila 2002, McGarigal and Cushman 2002, Fahrig 2003). The general finding of these studies has been that fragmentation resulting from habitat destruction often leads to a decline in species

richness and/or diversity. Often a decline in species richness or diversity in fragmented landscapes is accounted for by the local extinction of species with ecological traits that include large home range size, aversion to the conditions found at habitat edges, poor dispersal ability, and/or low habitat versatility (Meffe and Carroll 1997). Not surprisingly, species that possess the opposite suite of traits may benefit from landscape fragmentation either directly due to the creation of new edge habitats or indirectly, due to release from competition with habitat-sensitive species.

While community-level studies of fragmented landscapes have been successful in documenting the pernicious effects of habitat destruction, researchers have less frequently employed the reverse strategy of studying focal species with known ecological attributes in an attempt to understand which of the features of both the organisms and the fragmented landscapes contribute the most to local extinction. Examples include work on small mammals (Bowers et al. 1996, Bowers and Dooley 1999) and grasshoppers (With and Crist 1995).

We examined the effect of landscape pattern on populations of two invertebrate generalist predators: the wolf spiders *Pardosa milvina* Hentz and *Hogna helluo* (Walckenaer). Most wolf spiders are vagrant epigeal predators on small invertebrates, including members of their own species. Because they dwell almost exclusively on the soil surface they are very sensitive to soil-surface conditions, particularly moisture and temperature. The major determinants of these abiotic conditions are the frequency of disturbance and the accumulation of vegetative litter. We designed a suite of experiments around this pair of species because they are common, represent contrasting ecological archetypes, naturally co-occur in agricultural landscapes, and are easily manipulated in field experiments. *Hogna* is much larger than *Pardosa* (approximately ten times the mass), and is relatively sedentary (Walker et al. 1999a). In prior research we have found that these two spiders exhibit very different suites of traits relating to habitat versatility and vagility (Walker et al. 1999a, 1999b, Marshall and Rypstra 1999a, 1999b, Marshall et al. 2002, Balfour et al. 2003). *Pardosa* fits the model of the 'weedy' species: it has broader habitat tolerances and readily exploits disturbed edge habitats, (Marshall and Rypstra 1999a, 1999b) and is an efficient colonist of new habitat patches (Marshall and Rypstra 1999a, 1999b, Marshall et al. 2000, 2002). *Hogna*, on the other hand, avoids disturbed substrata, (Marshall and Rypstra 1999a, 1999b), and takes longer to colonize new habitat patches (Marshall and Rypstra 1999a, 1999b, Marshall et al. 2000, 2002).

We set out to test the relative importance of each of three correlates of habitat fragmentation (area reduction, area subdivision, and edge-to-core ratio) in determining the population-level response of two species with documented ecological differences. Our study consists of three different experiments, each designed to test the effect of a different aspect of habitat fragmentation. We predicted that *Hogna*, being larger, more habitat selective, and a poorer colonist (when compared to *Pardosa*) would respond negatively to increasing landscape patchiness. The behavioral mechanisms that explain these differences are *Hogna*'s aversion to barren substrata (Marshall and Rypstra 1999b, Marshall et al. 2000) and lower vagility (i.e. the frequency, duration and speed of locomotion; Walker et al. 1999a). We predicted that *Pardosa* would benefit from the same process as a result of decreased predation pressure by *Hogna*. We also set out to test which of three correlates of landscape fragmentation (area reduction, decreased connectivity and increasing edge/core ratios) had the greatest effect (if any was observed) on these two species.

We performed our experiments in replicated 0.42 ha experimental soybean fields where the two spider species occur naturally (Marshall and Rypstra 1999a, 1999b, Marshall et al. 2000). Row crops such as soybeans are especially well-suited for addressing landscape-level questions because they are grown in large monocultures, making it easy to experimentally impose spatial pattern (Kareiva 1985, Marshall et al. 2000). Our research has shown that both *Hogna* and *Pardosa* are found at higher densities on soil covered in vegetative debris (i.e. crop waste) and that *Pardosa* is more abundant than *Hogna* at all times of the year (Marshall and Rypstra 1999b, Marshall et al. 2000). We exploited the spiders' preference for litter-covered substrata as a tool to generate spatial pattern in our fields. We created islands of enhanced habitat within the fields and tilled barren buffer areas around each. Our intent was to present a two-element landscape to the spiders: enhanced microhabitat islands against a barren, disturbed background. Based on prior research we assumed that the surrounding agricultural landscape (made up of non-manipulated soybean fields, mowed areas, and woodlots) would serve as a source for immigrant spiders as well as a sink for spiders emigrating from our experimental landscapes (Marshall et al. 2000).

Methods

All research we report on here was conducted in the experimental soybean fields at the Ecology Research Center, Miami University, Butler County, Oxford, Ohio, USA (Fig. 1). The experimental fields at the Ecology Research Center (ERC) were established in 1994 under two contrasting cultivation regimes: conventional vs conservation tillage. In conservation tillage, herbicides are used to control weeds rather than tilling and the soil surface is only disturbed enough to plant the seeds. We found that fields maintained under a conventional tillage regime have lower densities of both *Hogna* and *Pardosa*

Fig. 1. Aerial photograph of the experimental fields in the spring of 1997. Photo taken at approximately 300 m altitude facing west. Each field is 60×70 m. Each field holds a replicate of either the area reduction experiment (the fields holding three large subplots) or the area subdivision experiment (the fields holding four subplots).

(Marshall and Rypstra 1999b, Marshall et al. 2000) because it decreased the depth and complexity of the litter layer that both species prefer. We used both types of fields in our experimental studies and account for background tillage regime statistically in our analyses.

We created the habitat islands by seeding the ground around the soybean plants with wild bird seed mix (containing millet, milo, safflower, wheat, and sunflower seed) and mulching it with wheat straw to create a litter layer. We have documented that these islands of enhanced habitat attract and retain greater numbers of both *Hogna* and *Pardosa* than even the relatively inviting conservation tillage fields (Marshall et al. 2000). Because we wanted to ensure that each experimental array had a population of both species, and because we have previously documented that *Hogna* population densities are limited by annual colonization, whereas *Pardosa* is not (Marshall et al. 2000) we added *Hogna* to each experimental patch at densities that approximate observed field densities (one *Hogna* per 1.44 m^2, Marshall et al. 2000). The *Hogna* used were captive-reared in the laboratory from field-collected females. We used lab-reared *Hogna* because it was impractical to collect them in the numbers needed. Prior research has shown that the addition of lab-reared *Hogna* can result in an increase in *Hogna* numbers in these experimental field plots (Marshall et al. 2000). We relied on natural immigration by *Pardosa* from the surrounding habitats for colonization. We have evidence from field studies that *Pardosa* densities observed in these fields are not limited by colonization thus there was no advantage to supplementing their numbers (Marshall et al. 2000).

We employed a standardized direct-observation census technique throughout this study. This technique was based on a restricted-area hand search of the soil surface. We defined and contained the census area using a sheet metal ring that enclosed an area of 0.75 m^2. We placed the ring on the ground and all standing vegeta-

tion within the ring was removed by hand. We then used a hand trowel to search through the detritus, earth clods, and soil fissures for all spiders. Because we used a restricted area search census method, all results reported herein are based on population densities per square meter. We also assumed that any change in subplot population density relative to the densities observed in the largest or least fragmented treatment unit in each experimental replicate represented a population-level response to the spatial patterns of the experimental landscape.

Area reduction

Between 9–11 June 1997 we created three arrays of habitat islands within six randomly-selected 0.42 ha soybean plots. Three of these replicate plots were in conventional tillage plots, and three were in conservation tillage plots. Each individual subplot consisted of a five by five array of 2.0 by 2.0 m habitat islands, each separated by 0.5 m strips of lower-quality (i.e. ambient soybean field) habitat. Each array was bounded by a tilled 3 m wide strip (Fig. 1). We added one *Hogna* to each island on 9 July 1997 to ensure a resident population in all subplots prior to habitat destruction. We randomly selected either 5 (20%) or 20 (80%) of the islands in a randomly selected array for destruction within each of the replicate soybean fields (with one no-destruction control array). We destroyed the selected habitat islands between the 29 July–1 August 1997 by removing standing vegetation by hand and covering the soil surface with a synthetic mulching fabric (Typar™ brand landscape fabric) to simulate habitat destruction. We used the fabric instead of tillage as we were unable to effectively till the individual habitat islands selected for destruction due to the spatial configuration of the subplots. Between the 30 August–1 September 1997 we censused all five remaining habitat islands in the 80% destruction treatments, and five randomly selected

islands in the other two treatment replicates using a restricted-area direct observation-search of 1.5 m^2 of the soil surface in each island for a total of 7.5 m^2 sampled per replicate. Data were analyzed using a split-plot ANOVA and means compared between treatments using Tukey's test (Neter et al. 1990).

Habitat subdivision

To keep total habitat area constant and alter the subdivision rate of each experimental landscape, we divided a 25 m^2 area into two, four, and eight equally-spaced squares, with a single 25 m^2 patch to represent a least-fragmented landscape (Fig. 1). We set up six replicates of this experiment in six of the soybean plots: three in conservation tillage plots and three in conventional tillage plots on 9 June 1997. The single-island landscape had one 5 × 5 m patch. The 2-square treatment had two 3.54 × 3.54 m islands, the 4-square treatment four 2.5 × 2.5 m islands, and the 8-square treatment eight 1.77 × 1.77 m islands. In principle, even the smallest squares in the 8-square treatment (approximately 3.13 m^2) should have been able to hold at least one *Hogna* each (Marshall et al. 2000). In the two, four and eight square treatments the individual mulched squares were three m apart. Each subplot was set up at least 10 m from the edge of the plots and from each other. We tilled a three m buffer strip of barren soil around all islands. We released *Hogna* on the 9th and 29th of July 1997 at the rate of eight per subplot. Thus the one-square treatment received eight *Hogna*, each of the squares in the two-square treatment received four *Hogna*, and so on. The buffer strip was again tilled on the 2–3 July 1997. We censused eight 0.75 m^2 samples of each of the subplots on the 23rd and 24th of August 1997. We did this by placing the sampling ring once in each of the patches in the eight-island landscapes, twice in each of the patches in the four-island landscapes, four times in each of the two-island landscapes, and eight times in each of the single island landscapes. Data were analyzed using a split-plot ANOVA and means compared between treatments using Tukey's test (Neter et al. 1990).

Edge/core habitat ratio

In 1998 we explicitly tested for an edge effect on *Hogna* and *Pardosa* numbers, while controlling for patch area and fragmentation. The three different landscape configurations were: 1) square, 5 × 5 m; 2) rectangle, 7.5 × 3.3 m; and long rectangle, 10 × 2.5 m. Each patch configuration was replicated once in each of three conservation-tillage soybean fields. These subplots were set up 8 June 1998 and we added eight *Hogna* to each subplot on 24 June 1998. We censused 6.75 m^2 in

each of the subplots using nine 0.75 m^2 sampling sites on 9 September 1998. Data were analyzed using an ANOVA, treating plot as a blocking factor. Means were compared between treatments using Tukey's test (Neter et al. 1990).

Results

Area reduction

There was a strongly-opposing response to habitat destruction by the two wolf spider species. Population densities of *Hogna* declined by approximately 75% with only a 20% reduction in area, while *Pardosa* numbers are almost twice as high in the 80% area reduction treatments as in the no-destruction controls. Based on Tukey's test there were significantly more *Hogna* in the controls than in the 20% or 80% destruction treatment (Fig. 2a, Table 1a), and significantly more *Pardosa* in the 80% destruction treatments than the controls or 20% destruction treatment (Fig. 2b, Table 1b). There was no significant effect of the background tillage regime, but there was a significant plot effect for *Pardosa*.
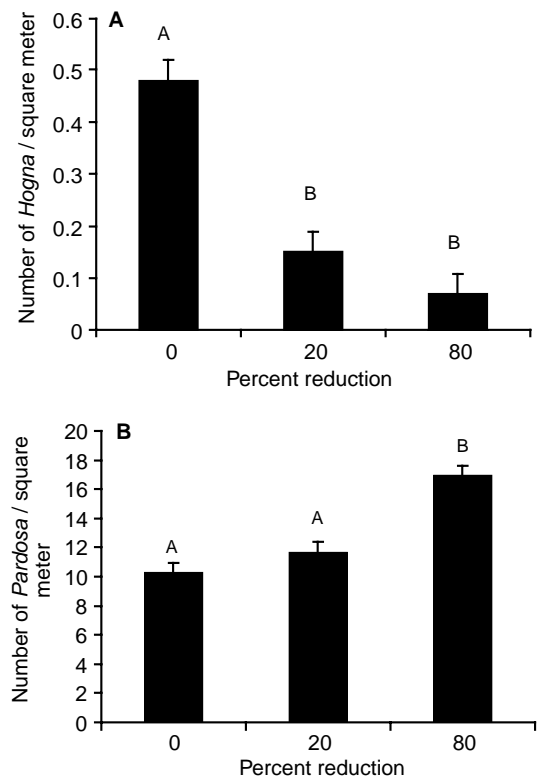

Fig. 2. (A) Response of populations of *Hogna* to area reduction. (B) Response of populations of *Pardosa* to area reduction. Numbers represent the number of spiders collected simultaneously per square meter. Error bars are the standard error of the mean. The letters represent Tukey's test with an alpha level of 0.05.

Table 1. Results of analysis of variance for habitat destruction. (a) *Hogna* m^{-2}, (b) *Pardosa* m^{-2}.

Source	Mean square	DF	F	P
(a)				
Tillage	0.000006	1,4	0.0004	0.9850
Plot (tillage)	0.05522	4,8	1.7103	0.2401
Habitat reduction	0.59684	2,8	39.969	<0.0001
Habitat reduction ×tillage	0.01778	2,8	1.102	0.3781
Error	0.008072	8		

*the denominator for all the tillage tests is the plot MS

Source	Mean square	DF	F	P
(b)				
Tillage	28.2251	1,4	0.5544	0.4979
Plot (tillage)	50.91	4,8	18.9874	0.0004
Habitat reduction	72.3544	2,8	26.9853	0.0003
Habitat reduction ×tillage	0.17087	2,8	0.0637	0.9387
Error	2.6813	8		

*the denominator for all the tillage tests is the plot MS

Habitat subdivision

There was a negative response by *Hogna* populations to the increasing subdivision of the habitat (Fig. 3a, Table 2a), and no significant response to habitat fragmentation by *Pardosa* (Fig. 3b, Table 2b). There was no effect of background tillage regime on *Hogna*, but there was a statistical interaction between habitat fragmentation and tillage regime observed for *Pardosa*.

Edge/core habitat ratio

Hogna populations had a negative response to increasing edge in the subplots (Fig. 4a, Table 3a), whereas *Pardosa* was apparently unaffected (Fig. 4b, Table 3b).

Discussion

We found clear support for our prediction that *Hogna* populations would decline with increasing fragmentation in the experimental landscapes. Our predictions were based on the result of field and laboratory studies of *Hogna*'s behavior and ecology. We did not directly observe the movement of *Hogna* in and out of the experimental landscapes, but the relative densities observed are consistent with its documented attributes. The response of *Pardosa* to the same landscape pattern was more ambiguous. In the area reduction experiment we found that even a slight (20%) loss of habitat led to a noticeable decline in numbers of *Hogna* and that *Pardosa* apparently benefited from the same treatment that had such a catastrophic affect on *Hogna*. The positive response to area reduction by *Pardosa* could indicate either a release from predation or competition with *Hogna*, or a positive response to the increased

availability of edges. The observation that *Pardosa* densities at the 20% destruction level did not increase in tandem with *Hogna*'s decline, however, argues against release from interspecific interactions as the primary
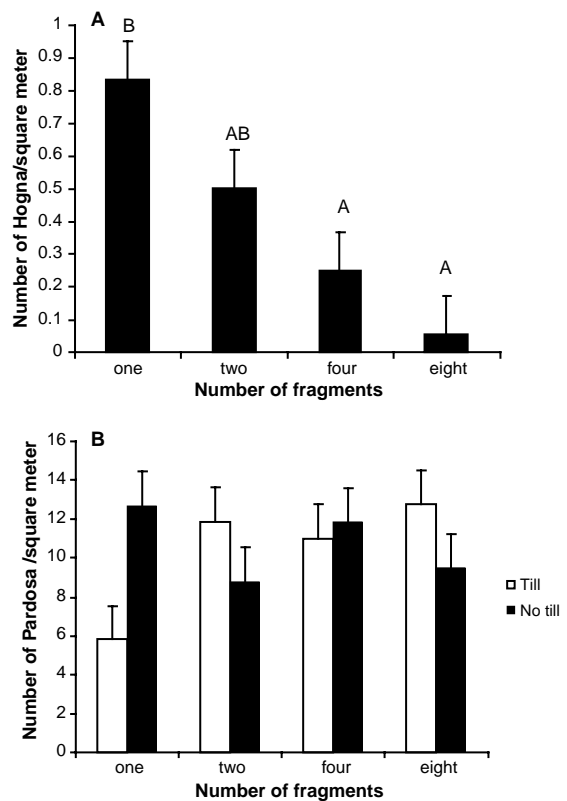

Fig. 3. (A) Response of *Hogna* to habitat subdivision. (B) Response of *Pardosa* to habitat subdivision. Numbers represent the number of spiders collected simultaneously per square meter. Error bars are the standard error of the mean.

Table 2. Results of analysis of variance for habitat subdivision. (a) *Hogna* m^{-2}, (b) *Pardosa* m^{-2}.

Source	Mean square	DF	F	P
(a)				
Tillage	0.0294	1,4	0.1233	0.7432
Plot (tillage)	0.23843	4,12	2.9250	0.0668
Fragmentation	0.67894	3,12	8.3288	0.0029
Fragmentation ×tillage	0.02261	3,12	0.2774	0.8407
Error	0.081517	12		

*the denominator for all the tillage tests is the plot MS

Source	Mean square	DF	F	P
(b)				
Tillage	0.72338	1,4	0.8693	0.4039
Plot (tillage)	0.83218	4,12	0.0893	0.9841
Fragmentation	5.83448	3,12	0.6260	0.6118
Fragmentation ×tillage	33.8746	3,12	3.6347	0.0449
Error	9.3198	12		

*the denominator for all the tillage tests is the plot MS

mechanism. In the habitat subdivision experiment there was a significant, negative response by *Hogna* to increasing habitat fragmentation coupled with no significant response by *Pardosa*. There was a significant interaction between tillage regime and fragmentation for *Pardosa*. This interaction appears to be due to the much lower densities of *Pardosa* found in the till, one fragment plots (where numbers are less than half those in the no-till plots, Fig. 3B). This may be attributed to the fact that there are greater ambient densities of *Pardosa* in the no-till plots than in the till plots. Thus, the positive effect of habitat subdivision would only be observable in the till plots. In the edge/core habitat ratio experiment, we again observed a steep and significant decline in *Hogna* densities, with no change in *Pardosa* densities. Taken together, these results tell us that: (1) *Hogna* responds negatively to any form of landscape fragmentation, (2) *Pardosa* may benefit from an increased prevalence of habitat edge, and (3) interspecific interactions are not an important interaction shaping the population-level response of these two species to landscape pattern.

We have evidence that immigration, emigration, mortality, and recruitment of both *Hogna* and *Pardosa* occur at the spatial and temporal scales tested (Marshall and Rypstra 1999b, Walker et al. 1999a, Marshall et al. 2000). Based on our knowledge of the model system we assume that the population declines exhibited by *Hogna* across treatments are the result of net emigration of patch residents into the surrounding landscape rather than differential mortality (e.g. predation). The strong, negative response of *Hogna* to area reduction, landscape subdivision, and edge/core ratio increase raises the possibility of some critical threshold in core habitat area needed to sustain a population. Similar threshold responses have been seen for other animal taxa subjected to experimental habitat fragmentation (With and Crist

1995, Wiens et al. 1997). In these cases the proposed mechanism is the 'percolation threshold', wherein dispersal is inhibited across the landscape by the increasing prevalence of gaps. We propose that the strong response exhibited by *Hogna* in all experiments is due to its behavioral aversion to the habitat edges
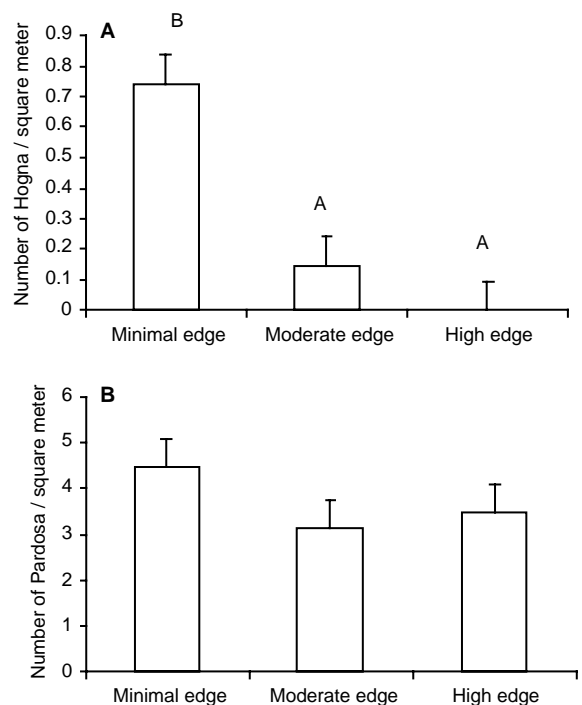

Fig. 4. (A) Response of *Hogna* to increasing patch edge/core habitat ratio. (B) Response of *Pardosa* to increasing patch edge/core habitat ratio. Numbers represent the number of spiders collected simultaneously per square meter. Error bars are the standard error of the mean.

Table 3. Results of analysis of variance for edge/core habitat ratio. (a) *Hogna* m^{-2}, (b) *Pardosa* m^{-2}.

Source	Mean square	DF	F	P
(a)				
Plot	0.05802	2,4	1	0.4444
Edge	0.46058	2,4	15.8759	0.0125
Error	0.1160	4		

Source	Mean square	DF	F	P
(b)				
Plot	6.7293	2,4	6.6449	0.0535
Edge	1.4491	2,4	1.4309	0.3398
Error	1.0127	4		

associated with habitat fragmentation. *Pardosa*, on the other hand, may be attracted to edge habitats. Studies of a congeneric, *Pardosa littoralis* Banks, have shown that members of this genus of wolf spiders will shuttle between different substratum types for foraging and thermoregulation (Morse 2002). This might also explain the response of *Pardosa* in the area reduction experiment: the relatively contiguous habitat found in the 0% and 20% reduction treatments (12×12 m) presented *Pardosa* with a more uniform habitat, lacking edges.

Not surprisingly, most experimental field studies of the influence of habitat fragmentation on ecological communities and specific animal taxa have been conducted using small mammals and terrestrial arthropods because of the more tractable spatial and temporal scales involved (Barret and Peles 1999, Debinski and Holt 2000). With and Crist (1995) used a combination of computer simulations and field experiments to look at the effect of habitat fragmentation on populations of two grasshopper species living in short grass prairie in Colorado. They found that the more vagile species maintained higher population densities at higher levels of fragmentation than the more selective, poor disperser. Researchers working with small mammals were the first to conduct experimental studies of the influence of landscape fragmentation on focal taxa. Bowers and Dooley (1999) have studied the differential response of meadow voles (*Microtus pennsylvanicus* Ord) and white-footed mice (*Peromyscus leucopus* Wagner) to experimentally patterned landscapes. Over many experiments Michael Bowers, James Dooley, Jr. and their collaborators have found that meadow voles respond positively to the same landscape fragmentation that has a negative impact on white-footed mice. The proposed mechanisms are similar to those we have observed with *Hogna* and *Pardosa*: white-footed mice are edge averse, and meadow voles exploit edges and disturbed 'matrix' areas.

Cook et al. (2004) have raised the issue of assumptions concerning matrix in studies of landscape ecology. They note that 'the matrix' is generally assumed to be inhospitable to the focal species and if this assumption is false it will lead to misinterpretation of experimental results. We propose that the same barren habitats that function as an aversive matrix for *Hogna* (i.e. functionally inhospitable) may be a useful, and even necessary, landscape element for *Pardosa*. This difference in habitat sensitivity apparently overrides the differences in habitat configuration tested in our three experiments. We found no revealing differences in *Hogna*'s strong negative response to increasing area reduction, subdivision, or edge.

Hogna and *Pardosa* present a revealing contrast of how two related, syntopic species will respond to habitat fragmentation as a result of their divergent ecologies. The very different responses of *Hogna* and *Pardosa* to landscape fragmentation are entirely consistent with what we know about their very different ecology and behavior.

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