Landscape Ecology vol. 11 no. 5 pp 299–306 (1996)
SPB Academic Publishing bv, Amsterdam

Effects of patch shape on the number of organisms

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Keywords: Patch shape, immigration, *oxidus gracilis,* millipede

Abstract

This study examined effects of habitat patch shape on the abundance of organisms. The effects of patch shape were considered in terms of (1) immigration and emigration of organisms, (2) the amount of available resources in a patch and *(3)* spatial and temporal heterogeneity of the organisms and environment. I hypothesized that (1) the number of organisms would increase as patch shape elongates because organisms are more likely to encounter an elongated patch, (2) the number of organisms in a patch would remain constant for all patch shapes where the number of organisms in a patch was limited by the amount of resources, because patch shape does not change the patch area that is directly associated with the amount of patch resources, and *(3)* spatial and temporal variation of the abundance of organisms would increase as patch shape elongates because an elongated patch is more likely to interact with the variable surrounding matrix.

Common millipedes, *Oxidus gracilis*, and their habitat, plywood boards of five shapes (width:length ratio; 1:1, 1:4, 1:9, 1:36, 1:144) with an area of 900 cm^2 were placed in forest and old field and the number of millipedes appearing under the boards was monitored. Significantly higher mean number of millipedes under the boards was observed at a patch with an elongated shape in the forest and the old field. A significant positive correlation was observed between perimeter length of a patch and the number of millipedes in the old field. The temporal and spatial variation of the number of millipedes was high in the old field. The spatial and temporal variation was higher for boards with elongated shape.

Introduction

A natural landscape consists of landscape elements which blend into one another, across ecotones of varying discreteness. These patterns reflect the interaction of organisms and the physical environment over time. Human activity has tended to fragment these natural patterns, replacing them with a built environment consisting of properties and linear elements which have little relationship to the former patterns. Natural landscape elements may persist as fragments or patches within this human dominated matrix. Clearly, conservation of the flora and fauna and their habitats requires an understanding, from both a theoretical and practical point of view, of the relationships between shape and size of these patches and the survival and abundance of organisms. While there have been a variety of studies of patch size and survival and diversity of plants and animals, there are relatively few studies of patch shape. This paper is a contribution to understanding the relation of patch shape and organism abundance.

In the most simple theoretical sense, patch shape is represented by the length of the perimeter of the patch. Holding area constant, a patch with a longer perimeter would likely have more organisms encounter it and therefore would contain more organisms. These shape effects were anticipated by Diamond and May (1976), Game (1980), Gutzwiller and Anderson (1992) and Stamps *et al.* (1987a, b) and have been demonstrated by Bruechner (1987) and Stamps *et al.* (1987 a, b). However, change in patch shape can theoretically have other effects on abundance which could produce contradictory results. For example, perimeter length and mobility would tend to increase density, unless emigration was stimulated more than immigration. In that case the population could be reduced within the patch. Change in patch shape will change the percentage of edge habitat. Increase in edge habitat might reduce the abundance of interior species. Patches with longer perimeters will encounter a greater variety of microenvironments in the matrix. Increased microenvironment heterogeneity could act positively or negatively on abundance. Thus, the theoretical relationships are probably not as straightforward as a mechanical model would imply. Experimentation is required to clarify these patterns.

The object of this paper is to report an experimental test of the relationship of patch perimeter length to organism abundance, using a common millipede and plywood boards as a model system. The boards were placed in hardwood forest and old field environments.

Methods

The study employed the ‘hot house millipede’ *Oxidus gracilis*. This millipede is cosmopolitan in distribution and is commonly found in green houses (Causey 1943). Adults range from 16 to 23 mm in length and 2.0 to 2.3 mm in width. Larvae emerge in early May in Georgia. The adult stage appears in mid July. Adult millipedes mate and lay eggs in July and August. Adults disappear by late August to early September.

Oxidus gracilis is found under leaves, rocks and logs where it can avoid heat and dryness during the day. At night when the humidity is high and temperature is low it leaves these refuges to forage and mate. The choice of a refuge mainly involves selection of a temperature and humidity (Cloudsley-Thompson 1951; Appel 1988) since the millipede lacks a waterproof epicuticular lipid layer which protects it from desiccation. Cloudsley-Thompson (1951) reported that the millipede prefers a high humidity (greater than 70%) and a temperature from 13 to 18°C. Cloudsley-Thompson also suggested that movement of the millipede was associated more with avoidance of undesirable environmental conditions than it was by a search for optimum conditions. **As** a member of the detritus feeding cryptozoa (Dendy 1895), O. *gracilis* lives in a food rich environment but one that can suffer extreme aridity in summer droughts. These environmental conditions cause either high mortality of millipedes or movement into long-term refuge sites. During and after a severe drought millipedes disappear, until the following year.

Studies of cryptozoa have been conducted by sampling soil and leaves directly (Savory 1971), by pit-fall traps or by laying boards on the ground (Cole 1946; Tarpley 1967). Boards provide an ideal experimental habitat for millipedes because the underboard environment has a higher humidity and lower temperature than the ambient environment and boards simulate objects in the millipede environment. Indeed, Tarpley (1967) reported that cryptozoan species were more attracted to boards than they were to natural environments.

In this study weathered plywood boards of 1 cm thickness were used to create habitat patches of different shapes. Five shapes were chosen but the area of the boards was held constant at 900 cm^2. Preparatory studies had shown that boards with an area of this size contained the greatest abundance of millipedes. The five shapes provided a graded series of boards with different perimeter lengths. The ratio of width to length of the shapes were 1:1 or 30 by 30 cm, 1:4 or 15 by 60 cm, 1:9 or 10 by 90 cm, 1:36 or 5 by 180 cm, and 1:144 or 2.5 by 360 cm.

The study was conducted on a farm in Madison County, Georgia. A randomized block experimental design was employed in a hardwood forest and an old field habitat. Three blocks (locations) were placed in each of the two environments and five boards were laid out randomly in each block in mid April, 1993, for a total of 15 boards per environment.

The ground surface appeared to be different in the two environments. The forest floor was covered by leaves, twigs and branches. There were no live herbaceous plants or grasses in the forest blocks. The old field vegetation was about seven years old, with *Lespedza sericea* and *Heterotheca subaxillaris* as dominant species. In contrast to the forest, the ground surface of the old field changed greatly over the growing season. In April much of the surface was bare ground or small plant rosettes. By midsummer the field was covered by dense vegeta-

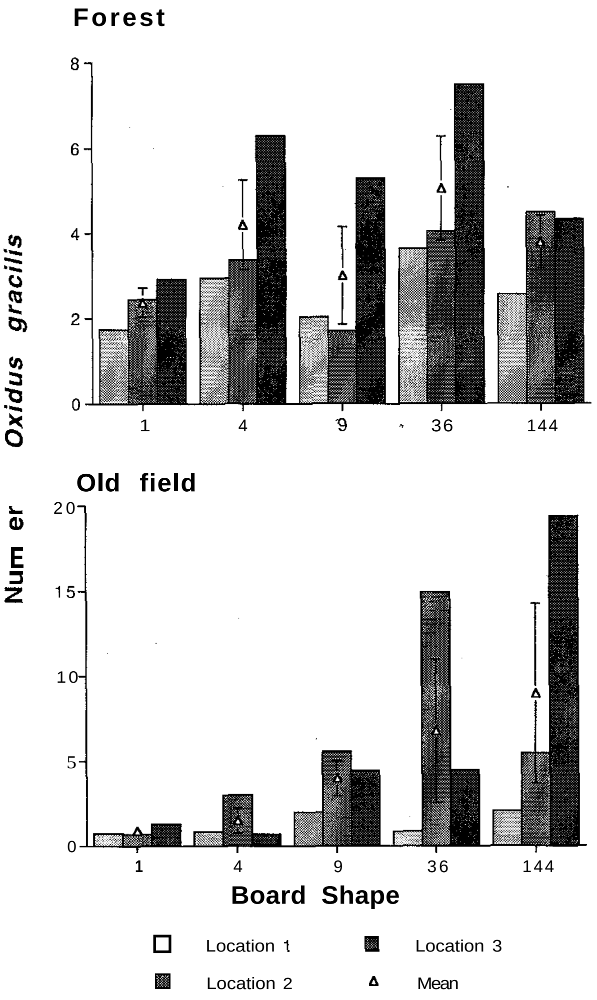

Fig. I. Pooled mean number of *O. gracilis* appearing under the five boards at three locations at two sites. The mean indicates the mean number of *O. gracilis* appearing at the three locations. The line indicates ± 1 standard error from the mean.

tion. In order to reduce the local microenvironmental variability at each board, the standing dead vegetation of the previous year in the old field and the leaf and stem litter under the boards in both locations was removed before the study began.

Millipedes were counted under boards around noon each sampling period. No millipedes were removed from a board and the board was replaced in the same position at each sampling period. The temperature and humidity under the board and in the ambient air near a board was measured at the same time the millipedes were censused. Humidity and temperature were measured only for the boards with the 1:1 shape ratio.

The research period was divided into three periods that approximately corresponded to the life cycle of the millipede. Period one consisted of 16 sampling days from May 2 to June 16 when most of the millipedes were larvae. At this time the mean temperature and humidity was 28.8°C and 47.5% in the forest and 32.9°C and 42.2% in the old field. Period 2 consisted of 40 sampling days from June 16 to July 31. Adult millipedes were present during this period. The mean temperature and humidity were 32.2°C and 45.8% in the forest and 38.4°C and 40.1% in the old field. Period 3 consisted of 18 sampling days from August 9 to August 26. The mean temperature and humidity were 30.5°C and 51.5% in the forest and 34.9°C and 39.4% in the old field.

Effects of patch shape were evaluated using the overall means for the entire season for an environment. Next, the effects were partitioned for location effect and for period effect. Because the distribution of millipedes under the boards were highly skewed, the Wilcoxon nonparametric test was used to test for difference in patch shape.

Results

Overall the mean number of millipedes was more variable and was greater in total amount in the old field (Fig. 1), but the difference in millipede abundance between the forest and field environments was not statistically significant.

The pooled mean number of millipedes appearing under the five board shapes were significantly different within both the forest and the field environment (Wilcoxon $p = 0.0388$ and $p = 0.0351$, in the forest and field respectively). In the forest the mean number of millipedes was highest for boards with a shape ratio of 1:36, followed by 1:4, 1:144, 1:9 and 1:1 (Fig. 1). In the field numbers were highest for the boards with a shape ratio of 1:144, followed by 1:36, 1:9, 1:4, and 1:1 (Fig. 1). The pooled mean number of millipedes was positively correlated with board length and perimeter length in the old field ($R^2 = 0.299$, $p = 0.0353$ and $R^2 = 2.90$, $p = 0.0385$ for board length and perimeter respectively). There were no significant correlations between millipede numbers and board width, length or perimeter in the forest.

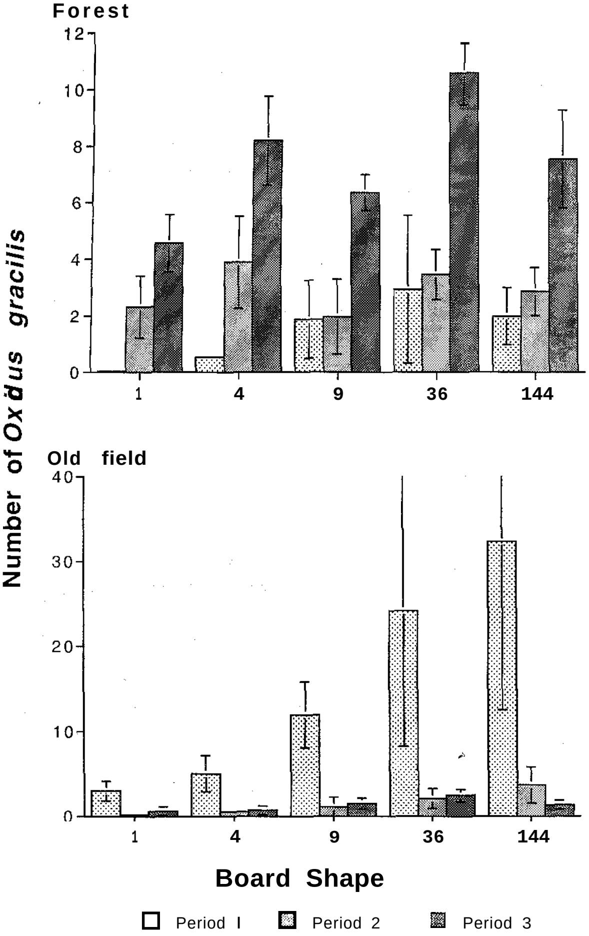

Fig. 2. Pooled mean number and ± 1 standard error of *O. gracilis* appearing under the five boards at three periods at two sites.

The location effect varied with environment (Fig. 1). The mean number of millipedes appearing under the boards was significantly different among the three locations in the old field ($p = 0.0406$), but was not significantly different at the forest locations ($p = 0.476$). In the old field, at location one, the number of *O. gracilis* appearing under boards with the five shapes was not significantly different. At location two the number of millipedes was significantly greater for boards with a shape ratio of 1:36. And at location three, millipede numbers were significantly greater for boards with the shape ratio of 1:144.

Millipede abundance also differed over time (Fig. 2). First, in the forest millipedes were most abundant during period three. In the old field millipedes were most common during period one.

Considering the board shape effects in the individual periods, during periods one and two there were no significant differences in millipede abundance for the five board shapes in either the forest or old field (Fig. 2). However, during period three in the old field the millipede numbers were significantly higher under boards with a shape ratio of 1:36 (Fig. 2), followed by 1:9, 1:144, 1:4 and 1:1 (Wilcoxon $p = 0.0454$).

Several significant interactions between location and time were also noted. A significantly positive correlation between numbers of millipedes and board perimeter length was observed at location one during period one in the old field ($R^2 = 0.935$, $p = 0.0072$). A single positive correlation was observed between numbers and board perimeter at location 3 during period 2 in the old field ($R^2 = 0.850$, $p = 0.026$). Millipede numbers were positively correlated with board perimeter length at location 2 during period 3 in the forest ($R^2 = 0.933$, $p = 0.0075$).

These results demonstrated patterns that were contrary to those expected from knowledge of the demography of the organism. It was anticipated that millipede numbers would be highest in period one and then would decline until millipedes disappeared in late August to early September. Rather, the observations suggested that numbers were influenced by environmental factors, which apparently obscured the expected trends. For example, in the forest (Fig. 3) the number of millipedes under the boards were associated with rain events. Number of millipedes encountered under boards was greater after most rains. This association was less clear in the old field (Fig. 4).

Discussion

This study supported the theoretical proposition that animal numbers should be correlated with length of the patch perimeter. However, the study also showed that this theoretical relationship may be confounded by factors associated with both the organism and the experimental environment.

First, millipedes appear under the boards because they are searching for suitable humidity and temperature. They seek refuge under boards during the day when the ambient environmental condi-

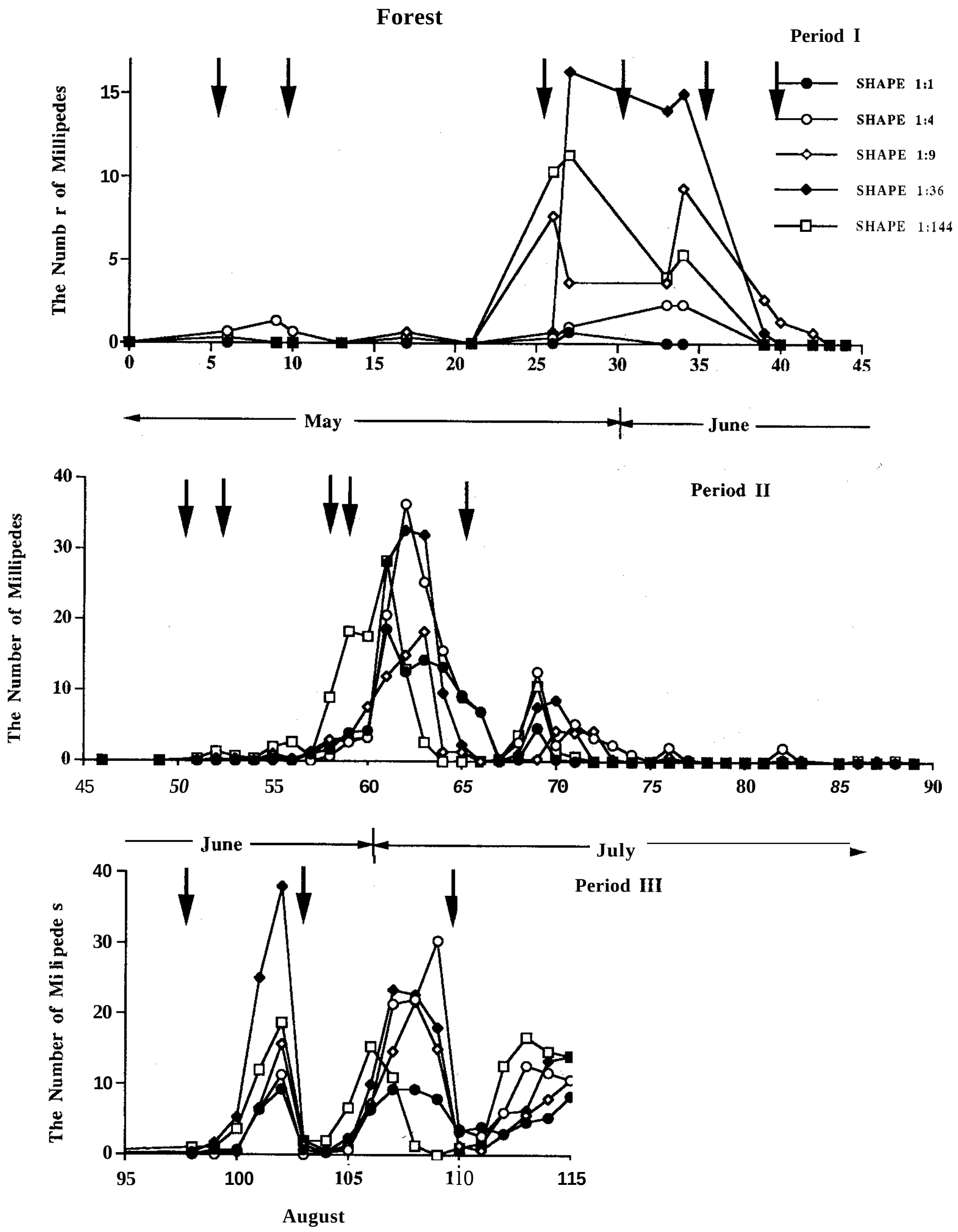

Fig. 3. The number of *O. gracilis* appearing daily under the five board shapes in the forest over the period of activity of the species. The arrow indicates a rainfall. The number on the X axis indicates days since the first day of observation.

tions are not suitable. However, there appear to not be resident populations of animals associated with a given location and therefore, with given boards. Millipedes are potentially highly mobile organisms. Several were traced moving over tens of meters during a night. Further, a mark and recapture study (personal observation) showed that no marked animals were recovered under the boards at the next day sampling period (marks remained on experimental specimens for over two weeks). Thus, the millipede populations appear to be both mobile and have a high turnover of individuals at a given location. This behavior makes the millipede an ideal organism for this type of study because this form of

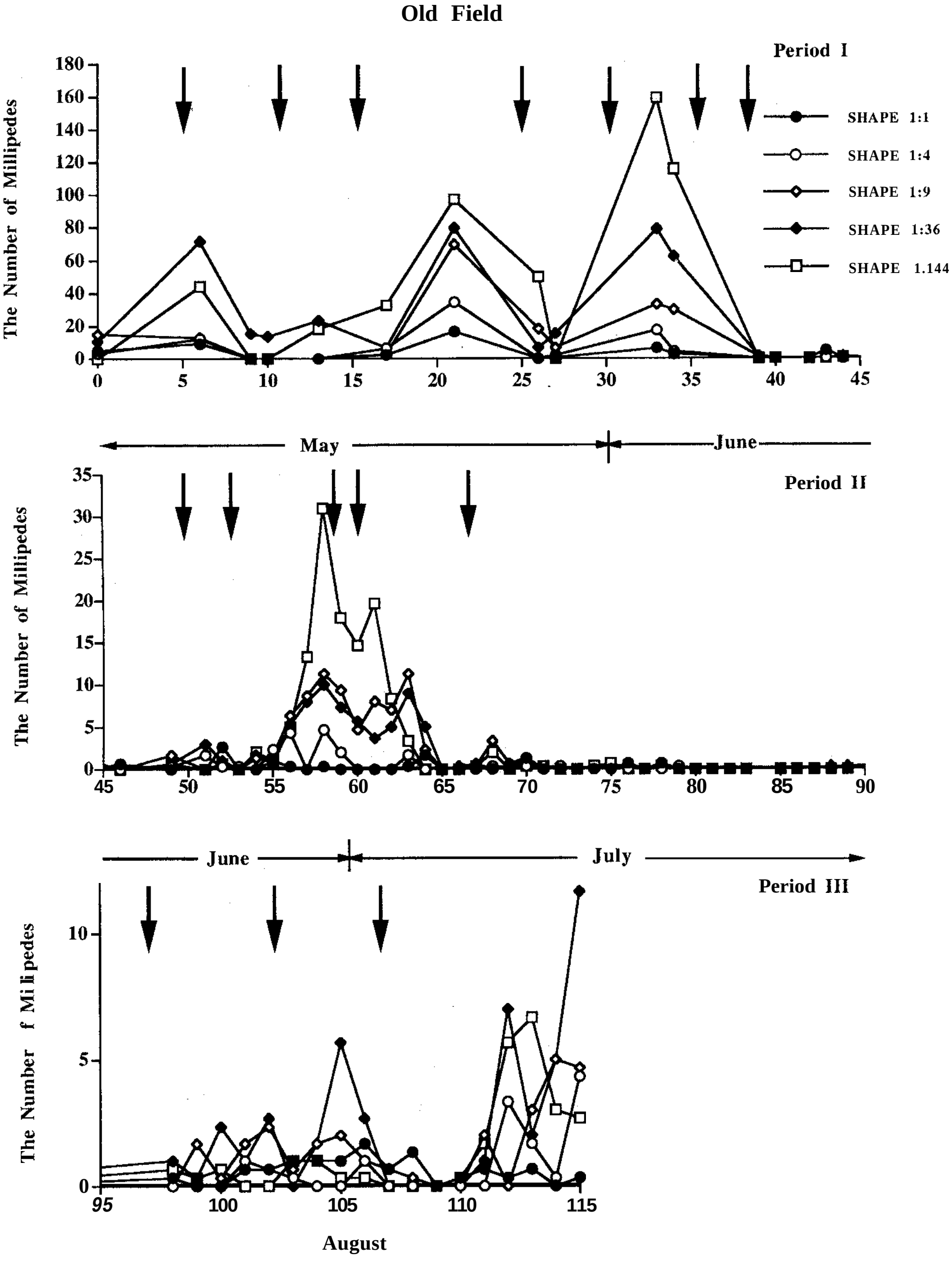

Fig. 4. The number of *O. gracilis* appearing daily under the five board shapes in the old field over the period of activity of the species. The arrow indicates a rainfall. The number on the X axis indicates days since the first day of observation.

movement is a prerequisite for the theory.

Second, in the forest environment the temperature and humidity conditions are more stable than in the old field and millipedes can find alternative refuges under logs, fallen branches and leaves and rocks. Stable environmental conditions and abundant alternative refuges obscured the relationship between board shape and millipede abundance in the forest environment. In contrast, in the old field few alternative refuge sites appear to be available and the environmental conditions on the soil surface are more variable. In this environment the expected perimeter-abundance relationships were observed more frequently.

The study concluded that there were significant patch shape effects on the abundance of millipedes, that a habitat patch with a high perimeter to area ratio is more likely to be located by mobile organisms and that a habitat patch with a high perimeter to area ratio is also more likely to be impacted by temporal and spatial effects from its surrounding environment. These conclusions imply that there may be an optimum habitat shape for this species since a larger perimeter to area ratio is positively related to organism mobility but negatively related to external environmental influence. A patch could become so elongated that it no longer retained an individual environment but was totally under the influence of its surroundings.

This trade-off could be important in conservation and management. A patch shape with a low perimeter to area would be preferable to sedentary and interior species because it would experience lower invasion from organisms in the matrix, it reduces emigration of interior organisms (Buechner 1987; Diamond and May 1976) and it may maintain a more stable interior environment within the patch. However, immigration and emigration of interior species is also necessary to maintain the viability of the populations in a patch (Game 1980; Hanski and Gilpin 1991; Pulliam 1988). A patch shape with a high perimeter to area ratio would be preferable for organisms that need immigration or emigration of individuals for their survival. High immigration rates may be important to reestablish a species in a patch.

The theory that the perimeter to area ratio of a habitat patch and organism abundance are directly correlated does not incorporate interconnections of patches by corridors. Corridors will probably alter the conclusions obtained in this study by enhancing specific types of mobility. However, corridors are also exceptionally elongated habitats, which, reasoning from the results obtained here, means that they are strongly influenced by environmental factors and contain little or no interior habitat. To place corridors in the theory will require further experimentation.

Acknowledgements

I greatly appreciate Dr. Frank Golley for his guidance, reviewing the manuscript, and providing access to the study site. I am deeply grateful to Nancy Laurenzo for her inspiration, field assistance, and support. I thank Margi Flood for her encouragement and support. My appreciation also is extended to Barbara Lockley for her support. This research is a part of a dissertation submitted to the University of Georgia in partial fulfillment of the requirements for Ph.D. degree. This research was partially supported by the Odum Foundation, Institute of Ecology, the University of Georgia.

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