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# FACTORS AFFECTING NEST LOCATION OF PRAIRIE VOLES (*MICROTUS OCHROGASTER*)

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The selection of a suitable nest (den) site should enhance individual survival and reproduction. We examined the effects of forage quality, vegetative cover, presence of preexisting underground nests, vole population density, and presence of conspecific nests on nest-site selection of prairie voles (*Microtus ochrogaster*). Vegetative characteristics did not predict the presence of nests; the only significant predictor was population density. Additionally, the presence of other currently occupied nests did not seem to affect placement of nests. In contrast to our expectation, voles did not nest in areas with preexisting underground nests. The presence of preexisting underground nests may have reduced the effects of vegetation on nest-site selection.

Key words: habitat quality, *Microtus*, nests, population density, prairie vole, rodent

The selection of a suitable nest (den) site within a habitat could enhance the survival and reproduction of individuals (Cowan 1987; Feldhamer et al. 1999). Because multiple factors are likely to affect the suitability of a nest site, nest-site selection can be a complex process. Factors that may affect the selection of a nest site could include food quantity and quality, risk of predation, and physical characteristics, for example, temperature and humidity around potential nest sites. Social factors such as the presence of competitors also can influence nest-site selection within a habitat. Most previous studies have focused on environmental factors (Berg and Berg 1998; Sherman 1984; Taulman 1999) but there is no previous study that takes both environmental and social factors into account.

We examined nest selection by the prairie vole (*Microtus ochrogaster*) in this study. Prairie voles occur in north-central North America (Hoffmann and Koeppl 1985) at population densities that vary from 11 to 624 animals/ha (Getz et al. 1993). This species has been described as a cooperative breeder in which young animals may delay dispersal because suitable territories are not available in high-density populations (Solomon 2003; Solomon and Getz 1997). These voles construct surface nests or underground systems with several burrows leading down to nest chambers (henceforth called underground nests). Underground nests are fairly extensive and located ~12 cm below the surface (Mankin and Getz 1994). In addition, prairie voles construct surface runways through vegetation or in the litter around their nests that allow rapid movement above ground. The construction of underground nests is energetically expensive (Ebensperger and Bozinovic 2000) and, while digging, voles would be at increased risk of predation (sensu Powell and Fried 1992). The purpose of this study was to determine the factors involved in nest-site selection in prairie voles, and how differences in population density affect selectivity and the distribution of nest locations. The factors that we examined included forage quality, amount of vegetative cover, presence of preexisting underground nests, population density, and presence of conspecific nests.

We tested the following hypotheses. First, we hypothesized that voles would preferentially nest in areas of high vegetative cover. Dense vegetation covering runways and nests offers protection from predators, for example, raptors (Baker and Brooks 1982; Birney et al. 1976). Dense vegetation also moderates microclimate (humidity and temperature) of a site (Getz 1965, 1971), thus reducing stress on animals. Second, we hypothesized that nests would be located in areas where sufficient high-quality food was available nearby. Prairie voles are herbivorous and require forbs in their diet (Batzli 1985) and breeding female voles, in particular, often spend a large proportion of their time in or near their nests soon after parturition (Sherman 1984). Thus, we expected voles to nest in areas with greater availability of high-quality food plants. Third, we hypothesized that prairie voles would use areas with preexisting underground nests to reduce the energetic cost and risk associated with underground nest and runway construction

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(Ebensperger and Bozinovic 2000; Powell and Fried 1992). Fourth, we hypothesized that prairie voles would be less selective in nest location when population densities were high than when densities were moderate. We expected that, at high densities, lower-quality sites would be selected after the choicest sites were preempted. Finally, we hypothesized that because male and female prairie voles are territorial (Getz et al. 1981), the distribution of nest sites would not be clumped, particularly at moderate population density.

## Materials and Methods

*Study site and enclosures.*—This study was conducted at Miami University's Ecology Research Center outside Oxford, Ohio (39°30′N, 88°44′W) during May–October 2001. Prairie vole populations were monitored in six 0.1-ha outdoor enclosures. These enclosures were made of 20-gauge galvanized steel panels that extended 75 cm above and 45 cm below ground with an electric fence extending about 15 cm above the top of the panels. These enclosures were sufficient to prevent movement of voles between enclosures (Cochran and Solomon 2000; Lorenz and Barrett 1990) and to prevent predators such as feral cats from entering enclosures. Although moderate-sized terrestrial predators could not enter enclosures, the enclosures contained northern short-tailed shrews (*Blarina brevicauda*), which may prey on nestling voles (Getz et al. 1992). In addition, raptors had access to voles in the enclosures. All voles were removed from enclosures before the beginning of this study but other rodents such as deer mice (*Peromyscus maniculatus*) were left in enclosures. A 1-m strip of bare soil was created by spraying herbicide around the inside of each enclosure wall to discourage voles from digging near walls.

*Experimental design.*—In late May, we measured characteristics of vegetation inside enclosures. Enclosures were then randomly divided into 2 treatments (moderate and high vole density). Density was manipulated by releasing either 5 (moderate density) or 12 (high density) voles of each sex into each enclosure ($n = 3$ enclosures/treatment) during early June 2001. All voles released were unrelated adults from a laboratory colony at Miami University consisting of $F_1$ or $F_2$ individuals originating from populations in southern Illinois. All voles were housed alone before release.

*Vegetative sampling.*—Vegetative sampling was conducted by using a nondestructive, point method (Barbour et al. 1999). Vegetation was sampled during 3 weeks before the release of voles to prevent changes in vegetation due to trampling of vegetation while we were livetrapping and radiotracking. We divided each enclosure into thirty-six 5 × 5-m cells. Each cell was further divided into 4 quadrants, and each quadrant was sampled once by using a point frame, constructed at the Miami University Instrumentation Shop, with a series of 10 points (pins), each approximately 5 cm apart; each pin was attached to a horizontal bar at the top of the frame. The entire point frame stood upright on metal supports. The point frame was placed in the center of each quadrant, and each pin was dropped vertically to the ground. As a pin touched a plant, we recorded the height of the intercept and the species of plant (Barbour et al. 1999).

Even though prairie voles eat a large amount of grasses and sedges, forbs tend to be their preferred forage (Cole and Batzli 1979). Our list of preferred forage (ragweed [*Ambrosia*], brome grass [*Bromus*], wild carrot [*Daucus carota*], bluegrass [*Poa*], goldenrod [*Solidago*], dandelion [*Taraxacum officinale*], and clover [*Trifolium*]) was based on previous studies of prairie vole food preferences (Cole and Batzli 1979; Jameson 1947; Lin and Batzli 2001). To determine if the quality of food or ground cover affected nest-site location, we categorized vegetation as monocots, dicots, preferred forage, or litter.

*Vole nest determination.*—Trapping began 2 weeks after the release of voles to monitor population density and to find nest locations. We followed the procedure described by Cochran and Solomon (2000), Hayes et al. (2004), and Lin et al. (2004). Sherman live traps (H. B. Sherman Traps, Inc., Tallahassee, Florida) baited with cracked corn (a low-quality food—Desy and Batzli 1989), set 5 m apart in a 5 × 5 array (25 trap stations per enclosure), were opened at 1900 h, checked at 0700, 1300, and 1900 h for 2 consecutive days, and checked and closed at 0700 h on the 3rd day every other week (7 trap checks total). For each capture, we recorded the individual's unique toe-clip number, sex, age class (juveniles: $\leq 20$ g, with gray pelage; subadults: 21–29 g; and adults: $\geq 30$ g, with brown pelage—Getz et al. 1987), reproductive condition, and location within the trapping grid. Males were categorized as reproductive or nonreproductive when testes were scrotal or abdominal, respectively. Females were categorized as reproductive when they were pregnant or lactating; otherwise they were considered nonreproductive.

We used 2 methods to follow reproductively active females to their nests: powder tracking or radiotelemetry. Individuals that weighed $<35$ g were dusted with ultraviolet reflective powder (Radiant Color, Richmond, California) as described by Lemen and Freeman (1985). We then followed powder trails to underground nest entrances or surface nests by using a battery-operated ultraviolet light (UVP, Inc., Upland, California). Females weighing $\geq 35$ g were fitted with PD-2C or PD-2CT radiotransmitters (Holohil Systems, Ltd., Carp, Ontario, Canada). Transmitters weighed 2.5–3.2 g. After their release, radio-collared females were tracked to their nests (underground nests and surface nests were both classified as nests although most nests were underground) with an ATS receiver (Advanced Telemetry Systems, Inc., Isanti, Minnesota) and Yagi antenna (Johnson's Telemetry, El Dorado Springs, Missouri) during the afternoon hours. Procedures in this study followed guidelines of the American Society of Mammalogists (http://www.mammalogy.org/committees/index.asp).

*Data analysis.*—We compared vegetative parameters between cells with and without nests. Because vegetation may have been somewhat different in species composition or percentage cover when some voles selected nest sites later in the season, we focused primarily on nest sites of founders. Percentage cover of each plant species was calculated for each quadrant from the vegetation samples by using the following equation (Barbour et al. 1999): percentage cover of species A = (number of pins touched by plant species A/10 pins) × 100. We determined percentage cover for each category (monocots, dicots, preferred forage, and litter layer) by summing percentage cover of all plant species in the same category to give an index of biomass for each category (thus, the values may be greater than 100). We used this index of biomass of the 4 quadrants within each cell for each category for statistical analyses. We also used the maximum plant height measured from each quadrant to calculate a mean height of vegetation for each cell.

A model containing these parameters (monocots, dicots, preferred forage, litter layer, and maximum height) was analyzed by logistic regression to determine if any of these variables predicted location of nests. Population density, either high or moderate, was used as a categorical variable in the model. We initially fit the full models to the data set, then removed nonsignificant terms sequentially. The significance of each term was assessed by the log-likelihood ratio (Sokol and Rohlf 1981) of the model analyzed with and without the term present. Model building was conducted hierarchically, with the highest order interactions removed 1st. Logistic regression was conducted by using the CATMOD procedure of SAS (SAS Institute Inc. 1985).

To determine if voles selected cells with preexisting underground nests, we compared the location of underground nests in 2001 to those

**Table 1.**—Source table for the logistic regression for location of nests in prairie voles. The regression was conducted to examine effects of population density, monocot biomass, dicot biomass, litter biomass, preferred food biomass, maximum height of vegetation, and all interactions of these variables with density to determine if any of these variables predicted nest location. We used backwards elimination to test for significance of the model.

| Effect removed | *d.f.* | $\chi^2$ | Probability |
|---|---|---|---|
| 1. Maximum height of vegetation × density × enclosure | 2 | 0.53 | 0.77 |
| 2. Dicot biomass × density × enclosure | 2 | 1.56 | 0.46 |
| 3. Maximum height of vegetation | 1 | 0.61 | 0.43 |
| 4. Litter biomass × density × enclosure | 2 | 2.52 | 0.28 |
| 5. Monocot biomass × density × enclosure | 2 | 3.50 | 0.17 |
| 6. Preferred food biomass × density × enclosure | 2 | 1.82 | 0.40 |
| 7. Density × enclosure | 1 | 1.77 | 0.41 |
| 8. Preferred food biomass | 1 | 0.04 | 0.84 |
| 9. Enclosure | 2 | 1.07 | 0.58 |
| 10. Monocot biomass | 1 | 0.40 | 0.53 |
| 11. Dicot biomass | 1 | 1.37 | 0.24 |
| 12. Litter biomass | 1 | 0.54 | 0.46 |

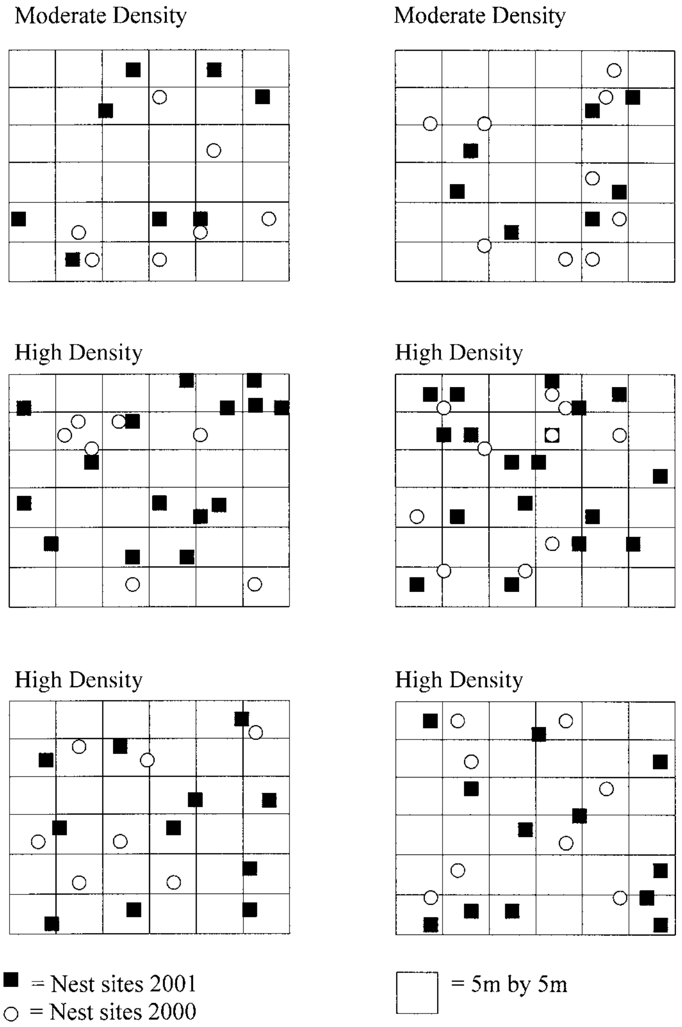

**Fig. 1.**—Diagrammatic representation of locations of nests of *Microtus ochrogaster* in moderate- and high-density populations in Ohio in 2000 and 2001. Moderate-density and high-density populations were founded by 5 or 12 adult voles of each sex, respectively.

from the same enclosures that had been located in 2000. We also analyzed data collected from 8 enclosures in 1994 and 1995. In both 1994–1995 and 2000–2001, voles had been removed from enclosures in autumn the previous year and then new populations were established in the following year, providing 2 independent data sets with which to examine the effects of preexisting underground nests. All enclosures in 1995 had high population densities (Cochran and Solomon 2000). We used a binomial test to determine whether underground nests were located in cells with or without underground nests from the previous year.

To determine whether the presence of conspecific nests affected nest-site location, we examined the distribution patterns of nest locations by using nearest-neighbor analysis (Krebs 1999). Expected values were generated by using a randomization procedure with 950 independent samples. We conducted nearest-neighbor analysis for data collected from these enclosures in 1994, 1995, and 2001.

## Results

*Vegetation.*—We found 10 species of monocots and 19 species of dicots in the 6 enclosures (Appendix I). Across enclosures, the indices of monocot and dicot biomass ranged from 77.5 to 200.0 and 0 to 202.5, respectively. The index of preferred food biomass ranged from 0 to 195.0, and that of litter ranged from 0 to 100.0. Maximum vegetation height varied from 56.2 to 135.0 cm. None of the vegetative parameters in the logistic regression model significantly predicted the location of nests nor did the interactions of vegetative variables with population density (Table 1).

*Population density.*—Population density was the only factor in the logistic regression that significantly predicted the probability of finding a nest site at that location ($P = 0.03$). The estimates of the 2 regression coefficients in this model were 1.36 (intercept) and −0.67 (density). From these numbers, we calculated the probability of a nest being present in a given cell as 0.20 at moderate density and 0.33 at high density. Thus, the effect of density increased the probability of a nest being present in a cell by ~50%.

*Presence of preexisting nests.*—In 2001, 77% of vole nests ($n = 13$) in moderate-density populations and 85% of nests ($n = 47$) in high-density populations were located in cells without preexisting nests. Overall, a significantly greater number of nests was found in cells without preexisting nests than in cells with preexisting nests (binomial test, $P < 0.00001$; Fig. 1). We found a similar result when using nest locations from 1995. During 1995, 77% of nests ($n = 73$ in high-density populations) were located in cells where there had been no nest during the previous year (binomial test, $P < 0.00001$).

Vegetative differences were found between cells with nests during both 2000 and 2001 and cells with nests during only 1 year. Cells with nests in only 1 of the 2 years had fewer dicots ($F = 3.37$, *d.f.* = 2, 45, $P = 0.04$) and less litter ($F = 3.86$, *d.f.* = 2, 45, $P = 0.03$) than sites with nests during both years. A nonsignificant tendency also was found for cells with nests in only 1 year to have more monocots than cells with nests in both

**Table 2.**—Ratios of observed to expected distances and confidence intervals for ratios between nests of nearest neighbors for *Microtus ochrogaster* in Ohio. Ratios less than the confidence interval indicate clumping; values greater than the confidence interval indicate overdispersion. All ratios are within confidence interval, indicating random placement. Enclosures were identified with either numbers or a number and letter combination.

| Year | Enclosure | Enclosure density | Observed/expected ratio | Confidence interval |
|---|---|---|---|---|
| 1994 | 1 | High | 1.05 | 0.69–2.28 |
| 1994 | 2 | High | 0.57 | 0.40–0.85 |
| 1994 | 3 | High | 0.67 | 0.47–1.24 |
| 1994 | 4 | High | 0.72 | 0.50–1.10 |
| 1994 | 5 | High | 0.49 | 0.31–1.90 |
| 1994 | 6 | High | 0.59 | 0.37–1.38 |
| 1994 | 7 | High | 0.49 | 0.34–0.85 |
| 1994 | 8 | High | 0.58 | 0.39–1.12 |
| 1995 | 1 | High | 1.12 | 0.81–2.38 |
| 1995 | 2 | High | 1.13 | 0.73–2.24 |
| 1995 | 3 | High | 0.96 | 0.65–1.62 |
| 1995 | 4 | High | 0.87 | 0.59–1.48 |
| 1995 | 5 | High | 1.00 | 0.68–1.72 |
| 1995 | 6 | High | 1.26 | 0.83–2.28 |
| 1995 | 7 | High | 1.14 | 0.74–1.86 |
| 1995 | 8 | High | 0.92 | 0.67–2.44 |
| 2001 | A3 | High | 1.15 | 0.75–2.30 |
| 2001 | A4 | High | 1.18 | 0.82–1.85 |
| 2001 | B1 | High | 1.38 | 0.87–2.92 |
| 2001 | B4 | High | 1.21 | 0.75–2.16 |
| 2001 | C1 | High | 0.96 | 0.61–1.65 |
| 2001 | C4 | High | 1.20 | 0.86–2.42 |
| 2001 | A1 | Moderate | 0.80 | 0.44–2.40 |
| 2001 | B2 | Moderate | 0.50 | 0.29–1.22 |
| 2001 | C2 | Moderate | 1.02 | 0.54–3.34 |
| 2001 | C3 | Moderate | 1.32 | 0.81–3.35 |

years ($F = 2.80$, *d.f.* $= 2, 45$, $P = 0.07$). No differences were found in preferred forage ($F = 0.57$, *d.f.* $= 2, 45$, $P = 0.57$) or maximum height of vegetation ($F = 0.61$, *d.f.* $= 2, 45$, $P = 0.55$).

*Presence of conspecific nests.*—Nearest-neighbor analyses showed that voles did not nest near other currently occupied nests (Table 2). In all populations during 2001, nest sites (29 nests in 4 moderate-density enclosures and 84 nests in 6 high-density enclosures) were randomly dispersed throughout the enclosures (Fig. 1). In addition, all nests were randomly dispersed in populations from 1994 (72 nests in 8 enclosures) and 1995 (73 nests in 8 enclosures). Thus, although voles did not nest near each other, they did not actively avoid nests of conspecifics.

## DISCUSSION

In contrast to our hypothesis that voles would preferentially nest in areas with high vegetative cover or sufficient high-quality food, our results showed that locations (cells) with nests did not differ in vegetative characteristics from those without nests in either high-density or moderate-density treatments. Vegetative characteristics, when considered alone, did not affect nest-site selection by prairie voles. Nevertheless, we did find that only locations of very high quality were used for 2 consecutive years. Locations with nests during both 2000 and 2001 had more dicots and thicker litter layers than locations with nests during only 1 year. This result suggested that vegetative characteristics did play a role in nest-site selection; however, their effects may have been compromised by other factors, such as preexisting underground nests. For example, if the attractiveness of high-quality locations, based on vegetative characteristics, were reduced by the presence of preexisting underground nests, then voles would nest in lower-quality locations. The interaction of these 2 factors could reduce the influence of vegetation.

Initially, we expected that voles would use sites with preexisting underground nests to decrease the risk and energetic cost associated with constructing new underground nests and runways (Ebensperger and Bozinovic 2000; Powell and Fried 1992). In contrast, prairie voles nested in areas where there had not been a preexisting underground nest. Preexisting underground nests may be perceived as unsuitable for several reasons. First, preexisting underground nests may contain parasite eggs from the previous occupants. Prairie voles are hosts to species of fleas, lice, ticks, and mites (Timm 1985), some of which may remain viable in underground nests after the original residents are gone. Previous studies of Brants's whistling rat (*Parotomys brantsii*—Roper et al. 2002) and Eurasian badgers (*Meles meles*—Butler and Roper 1996) suggest that periodic switching from one nest chamber to another decreases the rate at which ectoparasites accumulate. Furthermore, parasitic infections can decrease an individual's reproductive success (Arnold and Lichtenstein 1993; Edwards and Barnard 1987; Kavaliers and Colwell 1993). Second, voles may choose a new location for their nests because there would be little or no accumulation of scent that may attract predators or conspecifics (Banks et al. 2002). Third, voles may establish new nests because predators may return to sites where they have successfully captured voles previously.

Two other studies also provided supporting evidence that prairie voles avoid preexisting underground nests. Getz and McGuire (1997) found that few vacated nests were occupied by new residents in an unenclosed population of prairie voles in east-central Illinois. Furthermore, when both parents died, prairie vole offspring did not remain in the natal nest (McGuire et al. 1993). These results, together with ours, suggested that the costs of using sites with preexisting underground nests outweigh the energetic expense and risks incurred by runway construction and nest excavation (but see studies where the costs involved in construction of another nest outweighs using a preexisting nest in other semifossorial rodents (degus [*Octodon degus*]—Ebensperger and Bozinovic 2000; pine voles [*Microtus pinetorum*]—Powell and Fried 1992).

One other possible explanation for our results was that vegetative characteristics were homogeneous throughout enclosures. If high-quality nest sites are readily available regardless of population density, then females may not have to be as selective as in areas where preferred nest sites are limited. We found a range in monocots, dicots, preferred food, and litter cover in our enclosures, showing that these vegetative parameters were not homogeneous. In addition, the lack of clumped nest sites in our study was consistent with the suggestion that suitable nest sites were not limited. Getz and McGuire (1997) also argued that high-quality habitat was not limiting in their unenclosed prairie vole populations.

Population density was the best predictor in our logistic model of the probability of a nest being at a particular location. When population density was high, there was approximately a 50% increase in the probability of finding a nest at a particular site. The influence of population density is not surprising because there were, on average, twice as many nest sites in high-density enclosures ($\bar{X} = 14$) than in moderate density enclosures ($\bar{X} = 7.25$). On the other hand, we found that nest sites were randomly distributed within each enclosure regardless of densities. The latter result suggested that the presence of conspecific nests did not affect placement of nests; voles neither avoided nor were attracted to conspecifics at moderate or high density.

In conclusion, our study indicates that despite the potential energetic demands of underground nesting, prairie voles do not use preexisting underground nests. The presence of preexisting underground nests at the study sites may have reduced the effects of vegetative characteristics on nest-site selection. Several further studies are necessary to gain a complete understanding of nest-site selection by prairie voles. One future study would be to examine the effects of vegetative characteristics in the absence of preexisting underground nests. Another study would be to determine the reasons for avoiding locations with preexisting underground nests. Furthermore, although we chose to use laboratory-reared voles to control for age, these animals may have missed some experience while growing up that may be important in selecting a nest site when they are adults. Thus, it may be useful to examine choices made by free-living voles.

In addition, vegetative cover may be a more important factor in selecting a site for a surface nest. The majority of the nests that voles occupied were underground so vegetation may not be as important as we originally had proposed. Factors other than those investigated in this study, for example, soil texture and moisture (Fisher and Anthony 1980; Rhodes and Richmond 1985), may influence selection of a suitable underground nest site, and should be incorporated into a future study. Finally, we have assumed that the selection of nest sites by prairie voles is an adaptive choice. A subsequent study examining the reproductive success of voles nesting at sites of different vegetative quality would be necessary to test this assumption (see Cowan 1987).

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## Appendix I

Species of monocots found in the 0.1-ha enclosures at Miami University's Ecology Research Center, Ohio, during May 2001 included bluegrass (*Poa*), brome grass (*Bromus*), crabgrass (*Syntherisma*), dropseed (*Sporobolus*), fescue (*Festuca*), onion (*Allium stellatum*), ryegrass (*Lolium*), switchgrass (*Panicum virgatum*), and timothy (*Phleum pratense*). Dicots found in those enclosures included bindweed (*Convolvulus arvensis*), blackberry (*Rubus*), wild carrot (*Daucus carota*), chickweed (*Cerastium velgatum*), rough cinquefoil (*Potentilla norvegicus*), clover (*Trifolium*), daisy fleabane (*Erigeron annuus*), dandelion (*Taraxacum officinale*), goldenrod (*Solidago*), horse nettle (*Solanum carolinense*), common milkweed (*Asclepias syriaca*), ox-eyed daisy (*Chrysanthemum leucanthemum*), wild parsnip (*Pastinaca sativa*), field pennycress (*Thlapsi arvense*), plantain (*Plantago major*), common ragweed (*Ambrosi artemsiafolia*), thistle (*Carduus*), violet (*Viola*), and yarrow (*Achillea millefolium*).