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Roads Alter the Colonization Dynamics of a Keystone Herbivore in Neotropical Savannas[1]

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ABSTRACT

Roads can facilitate the establishment and spread of both native and exotic species. Nevertheless, the precise mechanisms facilitating this expansion are rarely known. We tested the hypothesis that dirt roads are favorable landing and nest initiation sites for founding-queens of the leaf-cutter ant *Atta laevigata*. For 2 yr, we compared the number of attempts to found new nests (colonization attempts) in dirt roads and the adjacent vegetation in a reserve of *cerrado* (tree-dominated savanna) in southeastern Brazil. The number of colonization attempts in roads was 5 to 10 times greater than in the adjacent vegetation. Experimental transplants indicate that founding-queens are more likely to establish a nest on bare soil than on soil covered with leaf-litter, but the amount of litter covering the ground did not fully explain the preference of queens for dirt roads. Queens that landed on roads were at higher risk of predation by beetles and ants than those that landed in the adjacent vegetation. Nevertheless, greater predation in roads was not sufficient to offset the greater number of colonization attempts in this habitat. As a consequence, significantly more new colonies were established in roads than in the adjacent vegetation. Our results suggest that disturbance caused by the opening of roads could result in an increased *Atta* abundance in protected areas of the Brazilian Cerrado.

RESUMO

Estradas podem facilitar o estabelecimento e a expansão de espécies nativas e exóticas. No entanto, os exatos mecanismos facilitadores desta expansão são raramente conhecidos. Nós testamos a hipótese de que estradas de terra são locais favoráveis à colonização e estabelecimento de ninhos por rainhas fundadoras da saúva *Atta laevigata*. Por dois anos nós comparamos o número de tentativas de fundação de novos ninhos (tentativas de colonização) em estradas de terra e na vegetação adjacente em uma reserva de cerrado no sudeste do Brasil. O número de tentativas de colonização nas estradas foi de 5 a 10 vezes maior do que na vegetação adjacente. Transplantes experimentais indicam que as rainhas fundadoras têm maior possibilidade de estabelecer um ninho em solos limpos do que em solos cobertos por serapilheira, mas a quantidade de serapilheira cobrindo o chão não explicou completamente a preferência das rainhas por estradas de terra. Rainhas que pousaram nas estradas estavam sob um maior risco de predação por besouros e formigas do que aquelas que pousaram na vegetação adjacente. Entretanto, a maior predação nas estradas não foi suficiente para compensar o maior número de tentativas de colonização neste habitat. Como conseqüência, um número significativamente maior de colônias novas foi estabelecido nas estradas do que na vegetação adjacente. Nossos resultados sugerem que as alterações ambientais causadas pela abertura de estradas podem resultar em um aumento na abundância de *Atta* em áreas protegidas do Cerrado brasileiro.

Key words: ants; *Atta;* Brazil*;* Cerrado vegetation; habitat disturbance; habitat selection; nest foundation; road impacts.

Roads are associated with a number of conservation problems, including the killing of wildlife by traffic, population fragmentation and isolation, and the spread of exotic species (Spellerberg 1998, Trombulak & Frissell 2000). However, while these effects can cause populations of some species to decline, other species may actually benefit from the ecological changes associated with roads and increase in abundance (Spellerberg 1998, Trombulak & Frissell 2000). The potential for roads to drive ecological changes has become a particular concern in protected areas and other regions of conservation interest, where roads are becoming an increasingly common feature of the landscape (Gutzwiller & Barrow 2003). For instance, in South America's highly diverse and threatened savannas, known commonly as the Cerrado (Ratter *et al.* 1997), roads have been shown to facilitate the establishment of exotic grasses that inhibit the regeneration of native trees (Hoffmann *et al.* 2004).

Leaf-cutter ants (*Atta* spp.) are one of the primary herbivores in Neotropical ecosystems (Wirth *et al.* 2003). While previous work has shown that large-scale disturbances to natural vegetation often favor leaf-cutter populations (Fowler 1983, Jaffe & Vilela 1989, Vasconcelos & Cherrett 1995), the impact of the disturbances caused by roads on *Atta* populations remains unexplored. Regardless of whether the impacts are positive or negative, the consequences for ecosystems in which leaf-cutters are found are likely to be large. Studies conducted in habitats ranging from rain forests to savannas have found that *Atta* species exert major impacts on vegetation structure and dynamics (Vasconcelos & Cherrett 1997, Farji-Brener & Ghermandi 2000, Rao *et al.* 2001, Hull-Sanders & Howard 2003, Wirth *et al.* 2003), soil properties (Farji-Brener 1992, Farji-Brener & Silva 1995), and nutrient cycling (Moutinho *et al.* 2003). Furthermore, a variety of animal species depend on leaf-cutter ant nests for shelter or food (Fowler *et al.* 1989).

Agriculture and other forms of human expansion have caused roads to proliferate throughout regions of limited human

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FIGURE 1. Leaf-cutting ant nest in one of the dirt roads that transverse the National Park of Emas, one of the largest preserve of Cerrado in Goiás, Brazil.

occupation, as well as national parks and other types of protected areas (Gutzwiller & Barrow 2003). While visiting several reserves of Cerrado in central Brazil, we noticed that mature *Atta* nests were particularly abundant in or on the edges of dirt roads (Fig. 1) but rare or absent away from them. Although a similar pattern has been observed in other locations (*e.g.,* Nogueira & Martinho 1983), the mechanisms responsible for this pattern remain unexplored. Here we test the hypothesis that dirt roads are favorable landing sites for *Atta laevigata* founding-queens, resulting in increased rates of colony initiation. In addition, we analyzed the importance of litter cover as a proximate cue in nesting-site selection by *A. laevigata*.

METHODS

STUDY SITE AND SURVEYS.—The study was conducted at the Estação Ecológica do Panga, a 404-ha reserve located near Uberlândia, Minas Gerais, Brazil (19°10′S, 48°23′W). The region has a subtropical climate characterized by a dry winter and a rainy summer (annual precipitation = 1600 mm). The soils range from well-drained red latosols to poorly drained hydromorphic soils. Most of the physiognomies that characterize the Cerrado biome are present in the reserve (Schiavini & Araujo 1989). Our observations and experiments were performed in the southern portion of the reserve, which is covered by *cerrado sentido restrito* and *cerrado denso* (*sensu* Oliveira-Filho & Ratter 2002).

A total of 11 transects were established in random locations along three dirt roads (two active, one abandoned). Each 50-m long transect was established parallel to the road, with a minimum distance of 50 m between any two transects. Transects were 12 m wide and divided into three 4-m wide sections: the central portion of each transect was the road itself, while the other two sections extended from the edges of the road into the Cerrado vegetation.

Following the mating flights that occurred in the afternoons of November 17, 2003 and November 5, 2004, we counted the number of attempts to found nests (hereafter "colonization attempts") in each section of each transect. Due to time constraints, only four transects were run in 2003, while in 2004 seven additional transects were established. To found a nest, the queen excavates the soil to a depth of approximately 20 cm. During this process, readily visible soil pellets are deposited around the entrance to the nest, which makes locating them straightforward. Although it is easier to find new nests in dirt roads than in the vegetation, we are confident that no nests from transects in the vegetation were missed, given that these transects were carefully surveyed several times by two observers until no more nests were discovered.

Transects were surveyed in the mornings following the mating flights, by which time queens had finished excavating their nests and sealed the nest entrance with soil. For the transects surveyed in 2004 only, we discriminated between successful and unsuccessful colonization attempts by assuming queens from those nests whose entrance was not sealed had been killed; we believe this assumption is justified because once a queen begins to build a nest she rarely abandons it to build another one (H. Vasconcelos, pers. obs.). When we observed the depredation of queens, we identified the predator and noted the portion of the transect where the predation event took place.

Finally, we measured litter cover, litter depth, tree canopy cover, and soil toughness for each section of each transect. Soil toughness was measured by recording the depth (in cm) to which a sharply pointed iron stake (1 m in length × 0.23 cm in diameter) dropped from a height of 1.60 m penetrated the soil ($N = 20$ points per transect). Prior to collecting soil toughness data the surface was cleaned of leaf-litter, grass blades, twigs, and other debris. Tree canopy cover was measured using a spherical densiometer at approximately 7 m intervals along each transect. Litter depth was measured in 20 randomly selected points in each section of each transect, and the resulting measurements combined to provide a mean value. Litter cover for each transect section was calculated as the proportion of points (out of 20) with litter. Since there was a strong and positive correlation between litter cover and litter depth ($r = 0.848$, $N = 22$, $P < 0.001$), subsequent statistical analyses were performed using only data for litter cover.

TRANSPLANT EXPERIMENTS.—On 5 and 17 November 2004 we experimentally tested whether founding-queens were more likely to build their nests in dirt roads or Cerrado vegetation, and how this was influenced by the presence or absence of litter cover in each site. The experiment consisted of gently placing individual queens that had just settled onto the ground, and had therefore not yet initiated nest excavation, into arenas consisting of a 1 × 1 m plywood frame placed firmly against the soil surface. The walls of the arenas were 15 cm tall, allowing queens to escape if the site was unsuitable for nest construction. We observed each queen for 30 min and recorded whether she started to build a nest or left the arena. We used a total of 12 arenas for the experiment: six in the road and six in the vegetation. Half of the arenas in each habitat type had bare soil (no litter), while the ground in the remaining arenas was covered with leaf litter; leaf litter for the roads came from arenas in the vegetation from which litter had been removed (*ca* 18 liter of litter/m^2). A different queen was used in each trial; trials in which the queen remained in the arena but did not excavate a nest were not included in the statistical analysis ($N = 2$ of 152 queens).

STATISTICAL ANALYSES.—We used ANOVA to determine the effect of habitat type on the number of colonization attempts, with habitat type (dirt road or Cerrado) as the main factor and transect as a blocking factor. Separate analyses were performed for data collected in different years of the study. Data on the number of colonization attempts per transect section (=200 m^2) were log (x + 1) transformed prior to the analyses.

Regression analyses were performed to determine the effect of tree cover, litter cover, and soil toughness on the number of colonization attempts within the Cerrado vegetation. We used simple linear regression instead of multiple regression analysis given the strong correlation between tree cover and litter cover ($r = 0.726$, $P < 0.001$). The number of colonization attempts in the sections of each transect covered by vegetation was expressed as a proportion relative to the number of colonization attempts in the road section of the same transect. In this way, we were able to minimize the effect of spatial variation in the number of colonization attempts. Data on tree canopy cover and litter cover were arcsine transformed prior to analyses.

We used the Mann–Whitney *U* test to determine if there was an effect of habitat on the intensity of predation on founding-queens, calculated as the proportion of queens killed. Differences in the number of queens excavating a nest versus leaving the arena, and how this frequency varied with the presence or absence of leaf litter, were analyzed using chi-square tests corrected for continuity or, when appropriate, with the Fisher's exact probability test.

RESULTS

HABITAT CHARACTERISTICS.—Dirt roads had no litter or tree cover. Litter cover in the adjacent Cerrado vegetation averaged 85.0 ± 3.5 percent SE, while tree canopy cover was 62.3 ± 6.0 percent. Mean soil toughness was three times greater in the dirt roads than in the adjacent vegetation ($F_{1,21} = 176.6$, $P < 0.001$).

COLONIZATION PATTERNS.—*Atta laevigata* colonization attempts were significantly more frequent in the dirt roads than in the adjacent vegetation in both years of our study (Fig. 2: 2003: $F_{1,7} = 9.7$, $P = 0.017$; 2004: $F_{1,21} = 97.8$, $P < 0.001$). In 2003, the average number of colonization attempts (per 200 m^2) was five times greater in the roads than in the adjacent vegetation (mean ± SE = 58.5 ± 11.3 versus 11.8 ± 3.6 colonization attempts, respectively). Similarly, in 2004 there were on average approximately ten times more colonization attempts in the roads than in the vegetation (29.2 ± 6.1 versus 3.0 ± 0.8 colonization attempts, respectively; Fig. 2).

Part of the variation in the number of colonization attempts within the Cerrado vegetation was explained by variations in tree cover, in litter cover, and in soil toughness. There were significantly more colonization attempts in areas with a sparser tree cover ($R^2 = 0.25$, $P = 0.018$), less litter cover ($R^2 = 0.27$, $P = 0.013$), and with a tougher soil ($R^2 = 0.27$, $P = 0.013$).

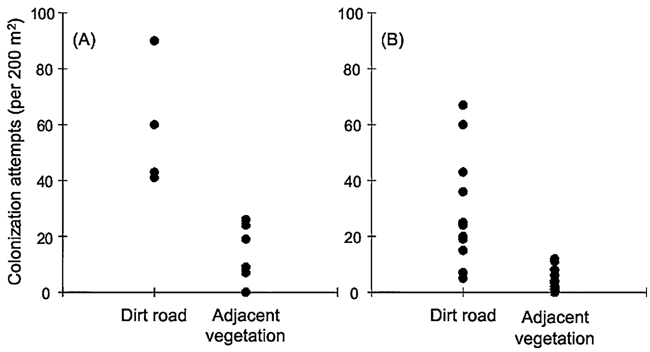

FIGURE 2. Number of colonization attempts by queens of *Atta laevigata* in dirt roads and adjacent Cerrado vegetation after the mating flights of November 17, 2003 (A) and November 5, 2004 (B). Each point represents data from a different transect or transect section.

The number of unsuccessful colonization attempts was significantly greater in dirt roads than in the vegetation (Mann–Whitney $U = 11.5$, $P = 0.007$; Fig. 3), suggesting that founding-queens were more likely to be attacked by predators in roads. In total, we observed 34 predation events; in our study area the most important terrestrial predators of *A. laevigata* queens were the scarabeid beetle *Canthon virens* (61.8% of observed predation events), *Atta* workers (25.5%), and other ants (14.7%), especially *Ectatomma* and *Pheidole*. Despite the higher incidence of predation, however, a significantly greater number of new nests were established in dirt roads than in the adjacent vegetation (mean ± SE: roads = 12.0 ± 2.5 nests; vegetation = 2.4 ± 0.7 nests; $F_{1,13} = 27.1$, $P < 0.001$).

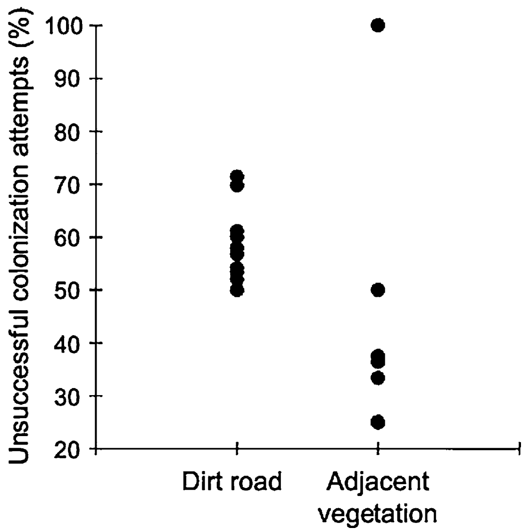

FIGURE 3. Percentage of the total number of colonization attempts in November 5, 2004, which were not successful (*i.e.*, nest entrance was not sealed). Each point represents data from a different transect or transect section. Only those with more than two colonization attempts were included in the analysis.

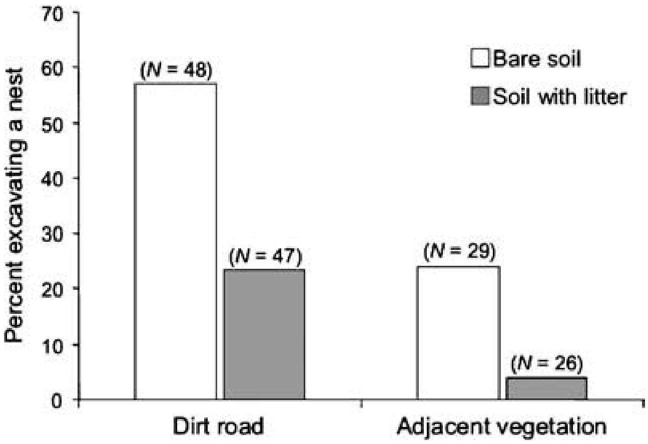

FIGURE 4. Percentage of *A. laevigata* queens excavating a nest in arenas with or without litter in two different habitats (dirt road and adjacent Cerrado vegetation).

TRANSPLANT EXPERIMENT.—Our experimental manipulation of litter cover revealed that the presence of leaf litter negatively influenced the likelihood of *A. laevigata* queens initiating a nest. In roads, significantly fewer queens started to excavate a nest in arenas into which leaf litter was added than in the no-litter arenas ($\chi^2 = 9.96$, $P = 0.002$; Fig. 4). Conversely, in the Cerrado vegetation significantly more queens started to excavate a nest in arenas without litter than in those in which litter remained (Fisher's exact probability test, $P = 0.037$). Irrespective of litter cover, there were proportionally more queens founding a nest in the arenas located in dirt roads than in those located in the adjacent vegetation (40.6% versus 14.5%; $\chi^2 = 9.91$, $P = 0.002$; Fig. 4).

DISCUSSION

Roads have been shown to facilitate the establishment and spread of both native and exotic species (Gelbard & Belnap 2003, Hoffmann *et al.* 2004), including ants (DeMers 1993, Farji-Brener 1996, Terranella *et al.* 1999, Forys *et al.* 2002). Nevertheless, the precise mechanisms facilitating this expansion are rarely known. Our results indicate that roads strongly influence the nesting behavior of founding-queens, resulting in higher colonization rates in roads despite elevated rates of predation.

Founding-queens of *A. laevigata* actively selected dirt roads for nest establishment at the expense of naturally vegetated areas. Similarly, studies with *A. sexdens* (Vasconcelos 1990) and *A. cephalotes* (Jaffe & Vilela 1989) have demonstrated that founding-queens prefer to nest in small clearings (both natural and man-made clearings for agriculture or urbanization) in forest vegetation. However, none of these studies have elucidated what cues attract *Atta* founding-queens to open habitats. Here we have experimentally demonstrated that *A. laevigata* queens strongly prefer to nest on bare soil than on soil covered with leaf litter, indicating that litter cover is one of the factors involved in the selection of dirt roads as nesting sites. Indeed, in several instances we have directly observed queens that naturally landed in the Cerrado vegetation walking towards a road, while the reverse was never observed. It must be stressed, however, that nesting-site selection was most frequently made while queens were in the air; that is, most queens directly target roads.

Newly mated queens of several ant species are attracted to areas of high light reflectance (Forys *et al.* 2002). *Atta laevigata* queens may therefore be attracted to dirt roads because they have more incident light and greater soil exposure relative to adjacent vegetated areas. Because most colonization attempts in roads took place along road edges and in close proximity to trees, it is also possible that the trees bordering roads are used as landmarks and visual cues by queens. Once on the ground, queens may also use light as microhabitat cue for nest-site selection. This conclusion is supported by the fact that even when litter cover conditions were held constant, significantly more queens founded nests in the experimental arenas located in roads than in those in the adjacent vegetation (Fig. 4).

The patterns of habitat selection we observed are probably not due to predator avoidance. In our study area, the major terrestrial predator of founding-queens was *Canthon virens*, a beetle specialized on *Atta* queens (Hertel & Colli 1998). This beetle was found more commonly on roads than in the adjacent vegetation. As a result, queens that landed on roads were at greater risk of predation than those that landed in vegetation. Nevertheless, greater predation in roads was not sufficient enough to offset the greater number of colonization attempts in this habitat. As a result, significantly more nests were initiated in the roads than in the vegetation. These results suggest that the greater numbers of mature leaf-cutter ant nests near roads and other clearings in vegetation observed in other locations (*e.g.,* Nogueira & Martinho 1983, Jaffe & Vilela 1989), are at least in part due to more queens dispersing into these areas. In addition, the early survival of colonies established along the margins of dirt roads may also be higher. Leaf-cutter ant colonies apparently require a certain degree of sunshine on their nest mounds (Weber 1972, Jaffe & Vilela 1989), and therefore nests established in open areas are likely to develop better than those established in more shaded sites. Furthermore, disturbance in Cerrado vegetation, caused by the opening of roads, is likely to enhance the establishment of herbaceous plants and pioneer trees. The former appear to be a key resource used by young *Atta* colonies as a substrate on which to grow their fungal gardens (Wetterer 1994), while pioneer trees are often preferred by more mature colonies (Farji-Brener 2001).

CONSERVATION IMPLICATIONS.—Although *A. laevigata* is a typical species of the Brazilian Cerrado, it is usually found at low densities in undisturbed areas (Schoereder 1998). However, the proliferation of roads in the Cerrado biome is likely causing an increase in leaf-cutter abundance, not only in protected areas but also at other sites with low levels of disturbance, given that the presence of roads leads to an increase in colonization rates and possibly also on survival rates of established colonies (*cf.* Wetterer 1994). This conclusion is consistent with the results of ongoing surveys of leaf-cutter nests in our field sites; the majority of nests are located in the portion of the preserve where the dirt roads are located, and only a few nests are found more than 25 m from a road (E. H. M. Vieira-Neto, unpublished data). In addition to increasing the local abundance of colonies, roads may also serve as corridors for the expansion of *A. laevigata*'s range. In fact, the recent record of this ant species in remote areas of the Amazon (Vasconcelos & Cherrett 1995) is likely due to the opening of roads through the formerly undisturbed forest.

Leaf-cutter ants are highly selective, and they can have a major influence on the demography of their preferred plant species. For instance, two studies have demonstrated that plant recruitment is reduced in areas of elevated *Atta* density (Vasconcelos & Cherrett 1997, Rao *et al.* 2001). Furthermore, nest construction and the storage of plant material affect the physical and chemical properties of soil (Farji-Brener 1992, Farji-Brener & Silva 1995), which can generate favorable microsites in which native and exotic plant species can become established (Coutinho 1982, Farji-Brener & Ghermandi 2000). An increased abundance of *Atta* in protected areas of the Cerrado, due in part to the mechanisms demonstrated here, could potentially influence the structure and dynamics of this highly diverse and endangered biome.

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LITERATURE CITED

COUTINHO, L. M. 1982. Aspectos ecológicos da saúva no Cerrado: Os murundus de terra, as características psamofíticas das espécies de sua vegetação e a sua invasão pelo capim gordura. Rev. Bras. Biol. 42: 147–153.

DEMERS, M. N. 1993. Roadside ditches as corridors for range expansion of the western harvester ant (*Pogonomyrmex occidentalis* Cresson). Landsc. Ecol. 8: 93–102.

FARJI-BRENER, A. G. 1992. Modificaciones al suelo realizadas por hormigas cortadoras de hojas (Formicidae, Attini): una revisión de sus efectos sobre la vegetación. Ecol. Austral 2: 87–94.

———. 1996. Posibles vías de expansión de la hormiga cortadora de hojas *Acromyrmex lobicornis* hacia la Patagonia. Ecol. Austral 6: 144–150.

———. 2001. Why are leaf-cutting ants more common in early secondary forests than in old-growth tropical forests? An evaluation of the palatable forage hypothesis. Oikos 92: 169–177.

———, AND L. GHERMANDI. 2000. Influence of nests of leaf-cutting ants on plant species diversity in road verges of northern Patagonia. J. Veg. Sci. 11: 453–460.

———, AND J. F. SILVA. 1995. Leaf-cutting ant nests and soil fertility in a well-drained savanna in western Venezuela. Biotropica 27: 250–253.

FORYS, E. A., C. R. ALLEN, AND D. P. WOJCIK. 2002. Influence of proximity and amount of human development and roads on the occurrence of the red imported fire ant in the lower Florida Keys. Biol. Conserv. 108: 27–33.

FOWLER, H. G. 1983. Distribution patterns of Paraguayan leaf-cutting ants (*Atta* and *Acromyrmex*) (Formicidae: Attini). Stud. Neotrop. Environ. 18: 121–138.

———, M. I. PAGANI, O. A. SILVA, L. C. FORTI, V. P. SILVA, AND H. L. VASCONCELOS. 1989. A pest is a pest is a pest? The dilemma of Neotropical leaf-cutting ants: Keystone taxa of natural ecosystems. Environ. Manage. 13: 671–675.

GELBARD, J. L., AND J. BELNAP. 2003. Roads as conduits for exotic plant invasions in a semiarid landscape. Conserv. Biol. 17: 420–432.

GUTZWILLER, K. J., AND W. C. BARROW JR. 2003. Influences of roads and development on bird communities in protected Chihuahuan desert landscapes. Biol. Conserv. 113: 225–237.

HERTEL, F., AND G. R. COLLI. 1998. The use of leaf-cutter ants, *Atta laevigata* (Smith) (Hymenoptera: Formicidae), as a substrate for oviposition by the dung beetle *Canthon virens* Mannerheim (Coleoptera: Scarabaeidae) in Central Brazil. Coleopt. Bull. 52: 105–108.

HOFFMANN, W. A., V. M. P. LUCATELLI, F. J. SILVA, I. N. C. AZEVEDO, M. S. MARINHO, A. M. S. ALBUQUERQUE, A. O. LOPES, AND S. P. MOREIRA. 2004. Impact of the invasive alien grass *Melinis minutiflora* at the savanna-forest ecotone in the Brazilian Cerrado. Divers. Distrib. 10: 99–103.

HULL-SANDERS, H. M., AND J. J. HOWARD. 2003. Impact of *Atta colombica* colonies on understory vegetation and light availability in a Neotropical forest. Biotropica 35: 441–445.

JAFFE, K., AND E. VILELA. 1989. On nest densities of the leaf-cutting ant *Atta cephalotes* in tropical primary forest. Biotropica 21: 234–236.

MOUTINHO, P., D. C. NEPSTAD, AND E. A. DAVIDSON. 2003. Influence of leaf-cutting ant nests on secondary forest growth and soil properties in Amazonia. Ecology 84: 1265–1276.

NOGUEIRA, S. B., AND M. R. MARTINHO. 1983. Leaf-cutting ants (*Atta* spp.) damage to and distribution along Brazilian roads. *In* P. Jaisson (Ed.). Social insects in the tropics, pp. 181–186. University of Paris, Paris.

OLIVEIRA-FILHO, A. T., AND J. A. RATTER. 2002. Vegetation physiognomies and woody flora of the Cerrado Biome. *In* P. S. Oliveira and R. J. Marquis (Eds.). The Cerrados of Brazil: Ecology and natural history of a Neotropical savanna, pp. 91–120. Columbia University Press, New York, New York.

RAO, M., J. TERBORGH, AND P. NUNEZ. 2001. Increased herbivory in forest isolates: Implications for plant community structure and composition. Conserv. Biol. 15: 624–633.

RATTER, J. A., J. F. RIBEIRO, AND S. BRIDGEWATER. 1997. The Brazilian Cerrado vegetation and threats to its biodiversity. Ann. Bot. 80: 223–230.

SCHIAVINI, I., AND G. M. ARAÚJO. 1989. Considerações sobre a vegetação da Reserva Ecológica do Panga (Uberlândia-MG). Sociedade e Natureza 1: 61–66.

SCHOEREDER, J. H. 1998. Nest density of leaf-cutting ants in natural ecosystems. Rev. Bras. Entomol. 41: 233–234.

SPELLERBERG, I. F. 1998. Ecological effects of roads and traffic: A literature review. Global Ecol. Biogeogr. Lett. 7: 317–333.

TERRANELLA, A. C., L. GANZ, AND J. J. EBERSOLE. 1999. Western harvester ants prefer nest sites near roads and trails. Southwest. Nat. 44: 382–384.

TROMBULAK, S. C., AND C. A. FRISSELL. 2000. Review of ecological effects of roads on terrestrial and aquatic communities. Conserv. Biol. 14: 18–30.

VASCONCELOS, H. L. 1990. Habitat selection by the queens of the leaf-cutting ant *Atta sexdens* L. in Brazil. J. Trop. Ecol. 6: 249–252.

———, AND J. M. CHERRETT. 1995. Changes in leaf-cutting ant populations (Formicidae: Attini) after the clearing of mature forest in Brazilian Amazonia. Stud. Neotrop. Environ. 30: 107–113.

———, AND ———.1997. Leaf-cutting ants and early forest regeneration in central Amazonia: Effects of herbivory on tree seedling establishment. J. Trop. Ecol. 13: 357–370.

WEBER, N. A. 1972. Gardening ants, the attines. Mem. Am. Philos. Soc. 92: 1–146.

WETTERER, J. K. 1994. Ontogenetic changes in forager polymorphism and foraging ecology in the leaf-cutting ant *Atta cephalotes*. Oecologia 98: 235–238.

WIRTH, R., H. HERZ, R. J. RYEL, W. BEYSCHLAG, AND B. HÖLLDOBLER. 2003. Herbivory of leaf-cutting ants: A case study on *Atta colombica* in the tropical rainforest of Panama. Springer-Verlag, Berlin.