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The Function of Hitchhiking Behavior in the Leaf-cutting Ant *Atta cephalotes*[1]

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ABSTRACT

In some leaf-cutting ant species, minim workers ride on the fragments of leaves as they are carried back to the nest from the cutting site. There is convincing evidence that these "hitchhikers" can protect the leaf carriers from attack by phorid (Diptera: Phoridae) parasitoids, but we consider the possibility of other functions for the hitchhiking behavior. It has been hypothesized that the hitchhikers (1) feed on leaf sap from the edges of the cut leaves; (2) ride back to the nest to save energy; (3) get caught on the fragments as they are cut, and hitchhike because they cannot (or will not) get off; and (4) begin the process of preparing the leaf to enter the fungal gardens in the nest, perhaps by removing microbial contaminants. We observed hitchhikers of *Atta cephalotes* in 14 nests at the La Selva Biological Station in Costa Rica. There was no difference in the proportion of leaf carriers with hitchhikers between day and night. Because the nests we observed were largely nocturnal, more than 90 percent of the hitchhiking occurred at night. The phorid parasitoids are usually considered to be diurnal, so the preponderance of nocturnal hitchhiking suggests other functions in addition to parasitoid defense. Hitchhikers spent more time in the defensive head-up posture during the day, but spent more time in the head-down posture at night. The head-down posture may indicate cleaning or other leaf preparation. The hitchhikers were never observed feeding on sap. Hitchhikers frequently got onto and off of the fragments, and so they were not "marooned." Few hitchhikers rode all the way back to the nest and were often moving on the leaf fragment; these observations make the energy conservation hypothesis less likely, although we cannot reject it. We conclude that parasitoid defense is an important function of hitchhiking but also that there are probably other functions when parasitoids are absent. Based on available data, the most likely possibility is preparation of the leaf fragment before it enters the nest.

Key words: Atta cephalotes; *Costa Rica; herbivory; hitchhiking behavior; leaf-cutting ants; parasitoid defense; phorid flies; tropical rain forest.*

The workers of leaf-cutting ants (Attini: *Atta* and *Acromyrmex*) are among the most polymorphic of any social insect (Weber 1972, Wilson 1980, Wetterer 1999), with a large range of continuously varying worker size. Differently sized workers exhibit different behaviors. For example, in *Atta* species the smallest workers ("minims") tend the fungal gardens and care for brood; medium-sized workers leave the nest to forage for leaves; and the largest workers act as soldiers (Weber 1972, Wilson 1980, Fowler 1983). One unusual behavior observed on foraging trails of some leaf-cutting ants is "hitchhiking," when one or more minims ride on the cut leaf fragments as they are carried back to the nest by larger workers.

There are 15 described species of *Atta* (Bolton 1995), and hitchhiking by minims has been reported in at least 7 of these: *A. capiguara* (Hughes & Goulson 2001), *A. cephalotes* (Lutz 1929, Stahel 1943, Eibl-Eibesfeldt & Eibl-Eibesfeldt 1967, Feener & Brown 1993), *A. colombica* (Feener & Moss 1990), *A. laevigata* (Erthal & Tonhasca 2000), *A. mexicana* (Feener & Moss 1990), *A. sexdens* (Wilson 1980, Bragança *et al.* 1998), and *A. texana* (Waller 1980, Fowler 1983). We know of no report of an *Atta* species without hitchhiking. We found less published information about hitchhiking in the 25 described species (Bolton 1995) of *Acromyrmex*, but it occurs in some (although not all) members of the genus. For example, hitchhiking occurs in *Ac. coronatus* (Wetterer 1995) and *Ac. niger* (Wetterer 1991), but not in *Ac. octospinosus* (Quinlan & Cherrett 1977, Wetterer 1991) or *Ac. versicolor* (Wetterer *et al.* 2001).

The leading hypothesis for the function of hitchhikers is defense against parasitoids, particularly phorid flies (Eibl-Eibesfeldt & Eibl-Eibesfeldt

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1967, Feener & Moss 1990, Erthal & Tonhasca 2000). Several phorids in the *Apocephalus attophilus* group (Brown 1997) attack leaf-carrying *Atta* workers by first landing on the leaf fragment (Feener & Moss 1990, Brown 1999). If there are minims hitchhiking on the fragment, they vigorously defend the leaf carrier from attacking phorids (Eibl-Eibesfeldt & Eibl-Eibesfeldt 1967, Feener & Moss 1990). The careful experiments and observations of Feener and Moss (1990) demonstrated that hitchhikers can successfully defend against these phorids.

Because the evidence for the defensive role of hitchhikers is strong, many recent authors have assumed that defense is the sole function of this behavior; however, a review of the literature reveals several additional functions that have been hypothesized for hitchhiking.

SAP FEEDING.—Workers of various sizes, including minims, forage for leaf sap outside the nest (Littledyke & Cherrett 1976, Stradling 1978). A majority of the metabolic energy of *Atta* workers comes from sap rather than from the symbiotic fungus (Bass & Cherrett 1995), and so liquid foraging may be an essential function for small workers. Hitchhiking minims could ingest sap exuding from the edges of leaf fragments as they ride.

ENERGY CONSERVATION.—Hitchhiking minims may ride back to the nest to save the energy of walking themselves (Feener & Moss 1990). This hypothesis requires some reason for the minims to be outside the nest, either along the foraging trail or at the cutting site. Possible functions for minims to leave the nest include sap feeding at the cutting site (see previous hypothesis) or communicating information about leaf choice to the cutting workers (North *et al.* 1999).

MAROONED ON FRAGMENTS.—Stradling (1978) suggested that the minims feed on sap at the cutting site and are "inadvertently isolated on leaf fragments as these are severed by the cutters." The minims then ride back to the nests because "they are likely to cling to the moving fragments to avoid being dislodged" (Stradling 1978).

LEAF PREPARATION.—Within *Atta* nests, minims process incoming leaves to prepare them for the fungal garden (Weber 1972, Wilson 1980, Fowler 1983); thus, it is possible that they also perform these functions while hitchhiking. Weber (1972) observed that hitchhikers lick the surfaces of the leaf fragments on which they are riding, and suggested that this is either to clean the leaf or to add enzymes to promote growth of the symbiotic fungus. Minims in the nest remove microbial contaminants from the fragments (Quinlan & Cherrett 1977), possibly by using the antibiotic produced by the recently discovered *Streptomyces* symbiont (Currie, Scott *et al.* 1999). Given the potential for devastation of the fungal gardens by contaminants (Currie, Mueller *et al.* 1999, Currie & Stuart 2001), it may be advantageous to clean the leaf fragments even before they reach the nest for further processing.

Although the presence of hitchhiking minims is often mentioned by observers of *Atta* foraging columns, there are relatively few quantitative estimates of the hitchhiking rate or of how the rate varies in space and time. To choose among the hypotheses for the function of hitchhiking, we estimated the following parameters for *A. cephalotes* (L.): (1) the rate of hitchhiking at foraging trails during both day and night. Phorid flies usually are reported to be active only during the day (Waller & Moser 1990, Orr 1992, Feener & Brown 1993, Tonhasca 1996), and thus the parasite defense hypothesis predicts that there should be less hitchhiking at night; (2) the behavior of the minims while hitchhiking on leaf fragments; and (3) the rate of hitchhiking near the nest entrance versus closer to the cutting site. If there is significant cost to locomotion, the leaf preparation and sap feeding hypotheses predict that hitchhiking would be concentrated near the nest.

MATERIALS AND METHODS

Observations were carried out at nests of *A. cephalotes* at the La Selva Biological Station, Heredia Province, Costa Rica. For a general site description, see McDade and Hartshorn (1994).

In December 1996, we chose 14 study nests in primary forest along the CCL, CES, SUR, and LOC trails (Fig. 1 of McDade & Hartshorn 1994). For each study nest, we selected the foraging trail that had the most worker activity for data collection. Data were collected from these nests from 10 to 14 December, but there was persistent rain on 8, 9, and 14 December. Since rainfall greatly reduced ant foraging (T. A. Linksvayer *et al.*, pers. obs.), the data presented herein came only from the relatively dry period from 10 to 13 December. For each date, data for a particular nest were collected either during the day (0800–1100 h) or at night (2000–2300 h). Day and night dates alternated for each nest.

We measured rates of foraging and hitchhiking at two locations for each nest: one where the selected foraging column entered the nest and another at 10 m along the column toward the foraging site. Foraging rate was recorded as the number of ants carrying a leaf fragment that passed a set point on the trail during a one-minute observation period. For each location, the foraging rate was recorded during five one-minute periods spaced one minute apart. Hitchhiking rate was measured at the same times as foraging rate, and was recorded as the number of laden foragers that carried leaf fragments with one or more hitchhikers.

Detailed observations of the behavior of hitchhikers took place between 3 and 14 December 1998. Seven nests were chosen on the basis of foraging trails that were observable all the way to the nest from the tree on which leaves were being cut. There were 22 different sets of behavioral observations, 12 at night and 10 during the day. Each observation period continued for one hour or until 100 hitchhikers had been observed, whichever occurred first. This resulted in an average sample size of 70 hitchhikers per observation (range = 27–100). Behavioral data were collected simultaneously for a nest by two observers, one positioned at the nest entrance and the other at the base of the tree on which the ants were foraging. We used flashlights to make nighttime observations. Direct light caused foragers to move away until an acclimatization period of approximately one-half minute when normal activity resumed. We directed the light beam so as to make the foraging column visible to us with as little direct light on the column as possible and waited to collect data until the foraging column had been illuminated for several minutes.

During preliminary observation, we defined four behavioral categories for the hitchhiking ants: (1) head up: with the head raised away from the leaf surface, mandibles open; sometimes more of the body was raised (Eibl-Eibesfeldt & Eibl-Eibesfeldt 1967, Feener & Moss 1990); (2) head down: with the head oriented toward the leaf surface, sometimes in contact with the surface. This behavior often included licking or antennating the leaf; (3) moving: walking across the leaf surface, or moving onto or off of the leaf fragment; and (4) neutral: not in motion and with head not obviously directed either toward or away from the leaf.

Laden foragers were observed as they crossed a fixed line across the foraging trail. As each leaf with hitchhikers passed the line, the behaviors of all hitchhikers were categorized into one of the four types. If there were too many foragers to record the behavior of all hitchhikers, we recorded the behavior of the first hitchhiker to cross the line after a three-second pause.

In 1998, we also followed individual leaf fragments as they were carried from the cutting site to the nest entrance. Laden foragers coming down from the trunk of the tree being attacked were marked on the gaster with a dot of white, water-soluble paint. Every 30 seconds, we recorded the number of hitchhikers on the leaf fragment of the marked workers.

STATISTICS.—We used mixed-model ANOVA to evaluate hitchhiking and foraging rates. Nest was treated as a random effect; day versus night and location on the foraging trail were treated as fixed effects (Bennington & Thayne 1994). To analyze the differences in behavior of hitchhikers, we used multivariate ANOVA (MANOVA) because the proportion of time spent in different behaviors is not independent.

RESULTS

There was much greater foraging at night than during the day for the 14 nests studied in 1996 (paired *t*-test: $t = 7.5$, $P < 0.001$). Every nest had more foraging at night (Fig. 1); daytime foraging rate was an average of 11.2 percent of the nocturnal foraging rate. In the six nests with two samples for both day and night, foraging rate was different during the two times (ANOVA: $F = 50.1$, $P < 0.001$; Table 1A). Foraging rate did not differ among individual nests and the interaction between time of day and nest was not significant (Table 1A).

Nocturnal hitchhiking rates (Fig. 1) differed among nests (ANOVA: $F = 6.0$, $P < 0.001$; Table 1B); average hitchhiking rates per nest ranged from 12.7 to 56.2 percent of laden workers. There was a marginally significant (ANOVA: $F = 3.92$, $P = 0.069$) trend for more hitchhikers on leaf fragments at the nest entrance (30.7 ± 3.5%; $\bar{x} \pm$ SE) versus 10 m away (23.9 ± 2.2%). The interaction between time of day and distance from nest was not significant (Table 1B).

There were only six nests with sufficient day foraging (>10 laden ants in 5 min) to allow a reliable measurement of diurnal hitchhiking rate. There was no difference between rates of hitchhiking during the day versus night (Fig. 2), whether measured among foragers at the nest entrance

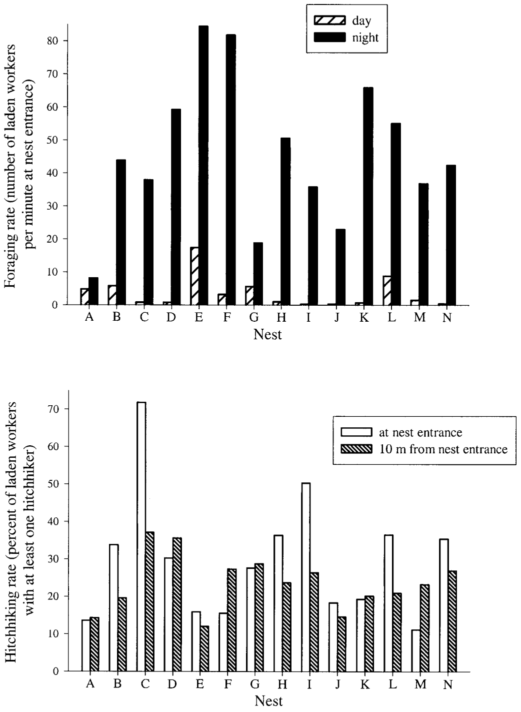

FIGURE 1. Foraging rate (top) and nocturnal hitchhiking rate (bottom) on *Atta cephalotes* trails in Costa Rica. Counts were made on the most active trail of 14 nests.

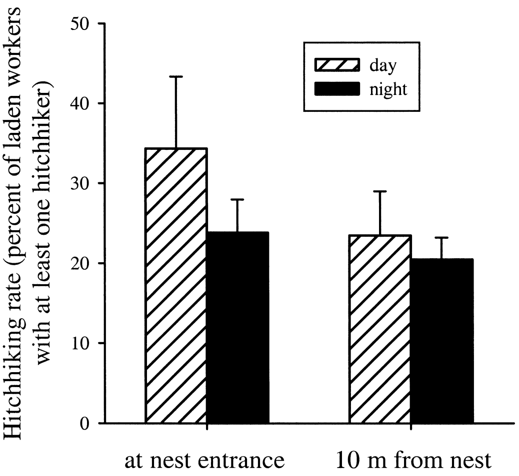

FIGURE 2. Nocturnal and diurnal hitchhiking rates measured at the nest entrance and along the foraging trail 10 m from the nest. Error bars show 1 SE. Only 6 of the 14 nests had sufficient daytime foraging to be used in the analysis. The difference between day and night was not significant at either location.

(paired *t*-test: $t = 1.3$, $P = 0.25$) or 10 m away from the nest (paired *t*-test: $t = 0.4$, $P = 0.7$).

The proportion of time that hitchhikers spent in the four behaviors (head up, head down, moving, or neutral) differed significantly between night and day (MANOVA: $F = 4.315$, $P = 0.016$), but not between the cutting site and the nest entrance (MANOVA: $F = 0.160$, $P = 0.956$). We performed post hoc comparisons for each of the four

TABLE 1. *Mixed model ANOVAs. See Figure 1 for means from these analyses. Top (A) is an analysis of foraging rate (number of laden foragers per minute on a single foraging trail) as affected by nest sampled (a random effect) and by time (day vs. night, a fixed effect). Only 6 of the 14 experimental nests had multiple samples at both times, and only these are included in the analysis. Bottom (B) is an analysis of nocturnal hitchhiking rate (percent of laden foragers with at least one hitchhiker on their leaf fragment) as affected by nest sampled (a random effect) and by position along foraging trail (at the nest entrance vs. 10 m from the entrance, a fixed effect). There were sufficient data for all 14 nests.*

Factor	df	Sum of squares	Mean square	Denominator mean square	*F*	*P*
A. Foraging rate						
Nest	5	1430	286	residual	2.22	0.120
Time (day vs. night)	1	10168	10168	nest × time	50.10	<0.001
Nest × time	5	1015	203	residual	1.58	0.240
Residual	12	1545	129			
B. Nocturnal hitchhiking rate						
Nest	13	7828	602	residual	6.01	<0.001
Position (nest entrance vs. 10 m from entrance)	1	641	641	nest × position	3.92	0.069
Nest × position	13	2127	164	residual	1.63	0.134
Residual	28	2804	100			

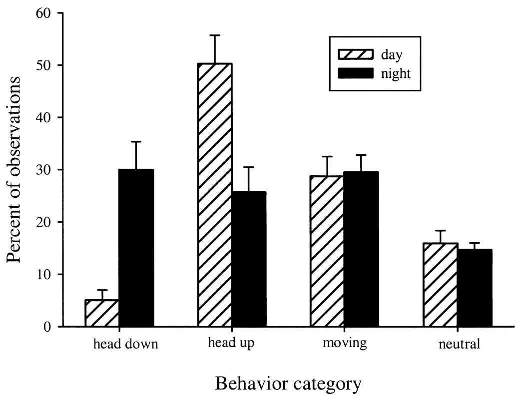

FIGURE 3. Comparison of nocturnal and diurnal behavior of *Atta cephalotes* hitchhikers. See text for full description of behavioral categories. There was a significant difference in behavior between day and night.

behaviors (Fig. 3); there was significantly more head-up behavior during the day (*t*-test: $t = 3.4$, $P = 0.003$) and significantly more head-down behavior at night (*t*-test: $t = 4.4$, $P = 0.001$). These two results remain significant even after Bonferroni adjustment of α to $0.05/4 = 0.0125$ (Scheiner 1993). There was no difference between night and day in the time spent moving (*t*-test: $t = 0.2$, $P = 0.9$) or in neutral position (*t*-test: $t = 0.4$, $P = 0.70$).

It was rare to be able to follow a leaf fragment from the cutting site to the nest entrance; fragments were sometimes lost by the observer in the foraging column, and workers often dropped leaves or lost their way. Figure 4 shows four fragments followed for the entire journey, which lasted from 17 to 28 minutes. Although the sample size was too small for statistical analysis, some results were clear. Each leaf fragment had hitchhikers at some point, but only for a minority of the time it was being carried (range for the four samples = 18–40% of time with a hitchhiker). It was common to have more than one hitchhiker per leaf, and in all four cases there were multiple times that hitchhikers either got onto or off of the fragment.

DISCUSSION

The rate of hitchhiking varied considerably among the nests we observed (Fig. 1), but generally 10–40 percent of laden workers had hitchhikers. Day and night estimates of hitchhiking rate did not differ significantly. Since the foraging rate was on average 11 times greater at night, we estimate that more than 90 percent of the hitchhiking activity was nocturnal. Other studies of *A. cephalotes* have found that the relative amount of nocturnal and diurnal foraging varied among nests and among seasons, but nocturnal foraging was often predominant (Lewis *et al.* 1974a, b; Wetterer 1990). If the sole function of hitchhiking is defense against diurnal parasites, why would hitchhiking occur so often at night?

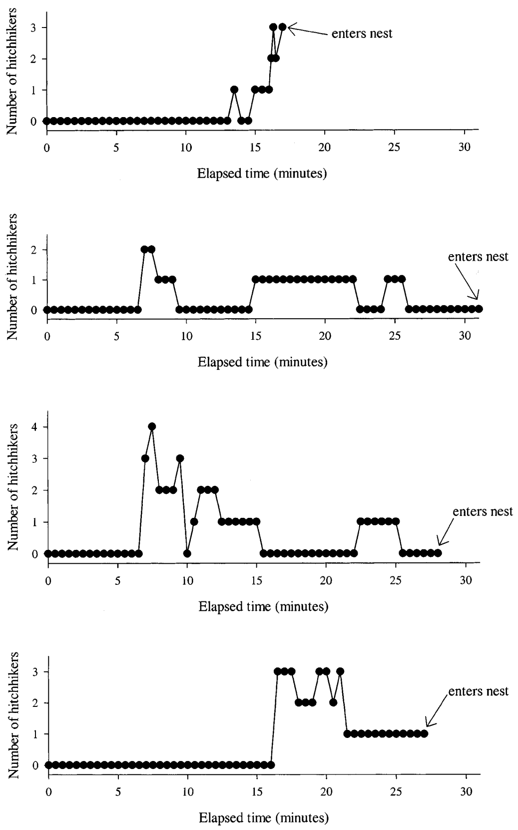

FIGURE 4. Number of hitchhikers on leaf fragments followed from the cutting site to the nest entrance. Data are presented for four cases in which the individual leaf-carrying ant could be followed for the entire trip.

Bragança *et al.* (1998) suggested that nocturnal hitchhiking in *Atta sexdens* could be a "stereotyped" defense behavior. Under this hypothesis, nocturnal hitchhiking would be a nonadaptive lack of reaction by minims to the difference in phorid abundance between night and day; however, the hitchhikers clearly behaved differently during the two times (Fig. 3). Feener and Moss (1990) demonstrated rapid adjustment of hitchhiking rate to phorid abundance: there was a significant increase in hitchhiking rate within 20 minutes of artificial introduction of phorids to foraging columns of *A.*

colombica. If hitchhiking rate can respond so quickly to changing phorid abundance, it is unlikely that nocturnal hitchhiking is due to the inability to detect or react to absence of phorids.

It may be that the nocturnal hitchhikers offer protection against nocturnal parasites. Phorids are usually considered to be active only during the day (Waller & Moser 1990, Orr 1992, Feener & Brown 1993, Tonhasca 1996), and for this reason nocturnal foraging by *Atta* has been proposed as a strategy to avoid diurnal phorid parasitism (Feener & Moss 1990, Wetterer 1990, Orr 1992, Rao 2000). There are few quantitative data on the daily activity patterns of phorids, but Orr's (1992) observations and experiments with artificial lights demonstrated the light dependence of at least one phorid species (*Neodohrniphora* sp.). Young (1986) trapped insects on flypaper near cacao (*Theobroma cacao*) flowers in Costa Rica and reported many phorids captured at night; however, the "nocturnal" period of Young (1986) was defined to include dusk and dawn and so these phorids could have been crepuscular rather than truly nocturnal. B. V. Brown and D. H. Feener Jr. (pers. comm.) have observed nocturnal attacks by phorids on leaf-cutting ants in Mexico and Argentina. It would be instructive to have more definitive information on diurnal patterns of other phorids that attack *Atta* foragers.

The difference in behavior of hitchhikers between day and night supports the possibility that parasite defense may not be the primary function of hitchhiking at night. During the day, hitchhikers were often in the head-up position (Fig. 3) that is characteristic of phorid defense (Eibl-Eibesfeldt & Eibl-Eibesfeldt 1967). This posture was significantly less common at night, which suggests that the hitchhikers did not defend against parasitoids as often at night. We agree with the suggestion of Bragança *et al.* (1998) that hitchhiking may have functions in addition to defense, especially at night.

SAP FEEDING.—Stradling (1978) showed that minims consume sap outside the nest; thus, another reason for minims to be on the leaf fragments could be to feed on sap. We, however, did not see hitchhikers licking sap from the cut leaf edge even though we specifically watched for this behavior. Also, if hitchhikers were feeding on sap on the leaf fragments, we hypothesized that the minims would travel shorter distances from the nest to climb onto the fragments. We found only limited evidence for greater hitchhiking rates at the entrance versus 10 m out. The difference was only marginally significant, and in 5 of the 14 nests there were more hitchhikers 10 m from the nest than at the entrance. This pattern is not consistent with the hypothesis that hitchhikers are feeding on leaf fragments as they ride. If the minims do forage for sap, it seems more likely that this occurs at the cutting site.

MAROONED ON FRAGMENTS.—Our data refute Stradling's (1978) suggestion that hitchhikers are marooned on the leaf fragments as they return to the nest. All four of the leaf fragments that we followed from the cutting site to the nest started the trip without hitchhikers, which therefore could not have been isolated on the fragments during the cutting process. We frequently saw hitchhikers come and go from leaf fragments (Fig. 4; Lutz 1929) and conclude that hitchhikers are not physically prevented from disembarking.

ENERGY CONSERVATION.—Feener and Moss (1990) calculated the energy that would be saved by minims riding back to the nest on a leaf versus walking and concluded that the savings in transport costs would be small. Also, the frequent observation of hitchhiker movement on the fragments (Fig. 3) and disembarkation well before the leaf fragment reached the nest (Fig. 4) do not seem consistent with energy conservation. We agree with Feener and Moss (1990) that this hypothesis is only weakly supported by available information.

LEAF PREPARATION.—The head-down behavior we observed in hitchhikers is consistent with the leaf cleaning behavior described by Stahel (1943) and Weber (1972). When we were able to get an unobstructed view, we saw that the head-down hitchhikers were touching their mouthparts to the surface of the leaf fragments and moving them across the leaf.

We found that individual leaf fragments were often without hitchhikers, but also that each fragment had hitchhikers at some point during the trip to the nest (Fig. 4). We hypothesized that leaf preparation would result in greater hitchhiking rates closer to the nest (as in the minim feeding hypothesis), but there was only weak support for this prediction. The licking behavior of the minims begins at the cutting site (Stahel 1943); so it may be that the process continues from the time of cutting and through the journey back to the nest. Although it seems costly to the nest to deploy minims all the way to the cutting site for this function, the benefit in preventing contamination of the fungal gardens

(Currie, Mueller *et al.* 1999, Currie & Stuart 2001) may be great enough to offset the cost.

The head-down behavior was relatively more frequent at night (Fig. 3). If hitchhikers concentrate on parasitoid defense during the day, the leaf preparation activity may necessarily be less common then. This may explain why Quinlan and Cherrett (1977) saw no licking behavior in hitchhikers of *A. cephalotes* during a limited number of daytime observations.

CONCLUSION.—Our data support the proposal that hitchhiking by leaf-cutting ant minims has functions in addition to defense. During the day, the hitchhikers are important in defending leaf-carrying workers from phorid parasitoids. The large majority of hitchhikers at our study site were out at night, when parasitoids presumably were not important. The hitchhikers had different behaviors on the leaf fragments during day versus night, which suggests that hitchhiking has different functions during the two times. Of the alternative possibilities for the function of hitchhiking, our data were most consistent with the leaf preparation hypothesis.

Further observations on the behavior of the minims, both at the cutting site and on the leaf fragments, would help clarify the possibly diverse reasons for hitchhiking. Comparisons among *Acromyrmex* species could also be particularly useful in understanding the origin and function of hitchhiking (Wetterer 1995, 1999), since only some *Acromyrmex* species hitchhike.

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