

Nest relocation in the slavemaking ants *Formica subintegra* and *Formica pergandei*: a response to host nest availability that increases raiding success

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Abstract Social insects typically occupy spatially fixed nests which may thus constrain their mobility. Nevertheless, colony movements are a frequent component of the life cycle of many social insects, particularly ants. Nest relocation in ants may be driven by a variety of factors, including nest deterioration, seasonality, disturbances, changes in microclimate, and local depletion of resources. The colony movements of slavemaking ants have been noted anecdotally, and in recent studies such relocations were primarily attributed to nest deterioration or shifts to overwintering locations. In this study we explore nest relocations in large colonies of formicine slavemakers which occupy stable and persistent earthen nest mounds. We investigate the hypothesis that colony relocations of these slavemakers are best explained by efforts to improve raiding success by seeking areas of higher host availability. Five summers of monitoring the raiding behavior of 11–14 colonies of the slavemakers *Formica subintegra* and *Formica pergandei* revealed relatively frequent nest relocations: of 14 colonies that have been tracked for at least three of 5 years, all but one moved at least once by invading existing host nests. Movements tended to occur in the middle of the raiding season and were typically followed by continued raiding of nearby host colonies. Spatial patterns of movements suggest that their purpose is to gain access to more host colonies to raid: the distance moved is typically farther than the mean raiding distance before the move,

which may indicate an effort to escape their local neighborhood. Furthermore, the mean distance of raids after relocation is shorter than the distance before relocation. For many slavemaking ant colonies, particularly those on the verge of relocating, raiding distance increased as the raiding season progressed. In addition, movements tended to be toward areas of higher local host density. Nest relocation is likely an important component of the ecology of slavemaking ants that contributes to the dynamic nature of their interaction with the host ant population.

Keywords Nest relocation · Slavemaking ants · *Formica subintegra* · *Formica pergandei* · Raiding behavior · Social parasite

Introduction

Ants have often been considered to be constrained in their movements by their dependence on a stationary nest. Although ant colonies were known to relocate nests, such movements were long assumed to be rare and a result of disturbance; however, some researchers suspected such colony movements were much more common than appreciated, and not simply a result of nest disruption (Smallwood, 1982a; Hölldobler and Wilson, 1990). An accumulation of studies either purposefully or incidentally documenting ant colony movements suggests nest relocations can be quite frequent in many ant species and an integral part of ant life histories (McGlynn, 2012).

Our understanding of the factors driving ant nest relocations remains far from complete, despite many hypotheses (Smallwood, 1982a; McGlynn, 2012). Some species exhibit movements to more favorable microclimates, particularly in response to shading (Smallwood, 1982b; Gibb

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and Hochuli, 2003). Ants that occupy ephemeral nest sites in the leaf litter like hollowed seeds, twigs, and dead leaves frequently move as their nest sites deteriorate (Foitzik and Heinze, 1998). Seasonal movements of colonies have also been observed (Herbers, 1985; Banschbach and Herbers, 1999). Depletion of local resources might seem like a reasonable explanation for colony movements; however, evidence for increased foraging success as a driver of nest relocation is weak, with the exception of nomadic army ants (McGlynn, 2012). Species interactions have also been proposed as driving colony movements. Though little evidence supports encounters with competitors as predictors of colony movement, a few species may be induced to relocate nests in response to attacks by army ants (Droual and Topoff, 1981; Droual, 1983) or slavemaking ants (Smallwood, 1982a; Topoff, et al., 1985; McGlynn, 2012).

Although slavemaking ants, like army ants, may be a driver of colony movements of their victims, little attention has been paid to the idea that slavemaking ants themselves may relocate their nests in response to resource availability. In the case of slavemakers, the resources they are exhausting are their supplies of new slaves rather than simply a food source [however, some captured brood is likely consumed instead of reared to maturity (Cool-Kwait and Topoff, 1984)]. Slavemaking ants raid colonies of a different host ant species and bring back pupae to become a work force in the slavemaker nest. The enslaved workers care for the slavemaker brood and forage outside the nest, while the slavemaker workers are primarily confined to the nest except during raids (Buschinger, 2009). Depending on how aggressively they exploit the host nests that surround them, slavemaker colonies could conceivably exhaust local sources of slave labor (Yasuno, 1964), thus forcing them to either undertake more distant raids (Bono et al., 2006a) or to relocate their nest to areas of unexploited hosts (Wheeler, 1910). Reduction in host density as a result of mortality of raided colonies is documented for myrmicine slavemakers like *Temnothorax duloticus* (Johnson and Herbers, 2006) and *Protomognathus americanus* (Foitzik, et al., 2009). Host colonies raided by formicine slavemaking ants can also suffer mortality (Bono et al., 2006a), though to a lesser degree than myrmicine victims.

A number of studies have documented the nest relocation of slavemaking ant colonies, but have not considered these movements in the context of the slavemakers' raiding behavior. Movements of the slavemaker *Protomognathus americanus* have been reported through indirect evidence, as new colonies appear in mapped plots where they did not previously exist (Foitzik et al., 2009), and for this species' diminutive colonies such movements have been attributed to the deterioration of their ephemeral nest sites in the litter layer (Scharf et al., 2011). Descriptions of movements by

this species have only been reported from lab settings (Al-loway, 1979).

The much larger formicine slavemakers which occupy more permanent excavated nest sites also exhibit nest relocations. Wheeler (1910) suggested that slavemakers relocate as host colonies move away from areas of heavy exploitation: "Then the *Polyergus*, too, finding no nests to pillage, are compelled to seek new field for their persistent and pernicious activities." However, when described by other researchers, moves by *Polyergus* appear to be coordinated by the slaves, which do the majority of transporting of brood and adults (Marlin, 1971; Topoff et al., 1985), suggesting that raiding success is not a factor motivating relocation. Topoff et al. (1985) observed movements by *Polyergus breviceps* slavemaker nests in response to intraspecific raiding, resembling frequent moves they noted in free-living host colonies after raids or other disturbances. Colony movement in slavemakers might also have a seasonal motivation. Kwait and Topoff (1983) described moves that occurred at the end of the season, to a so-called overwintering site. In these cases, *Polyergus lucidus* did participate in transporting adult slaves, but only after the movement by slaves was already underway. Likewise, Wheeler (1910) also suggested a seasonal component of movements, noting that the facultative slavemaker *Formica sanguinea* maintains summer and winter nests.

A few anecdotal accounts suggest movements of slavemakers in response to the availability of hosts. Wheeler (1910) reported finding a *Polyergus bicolor* slavemaker nest vacated several days after intense raiding of local host nests. Talbot and Kennedy's (1940) account of the behavior of *Formica subintegra* reports that the slavemakers frequently shifted location throughout the raiding season, not simply at the season's end, though the moves themselves were not witnessed.

As McGlynn (2012) notes, our knowledge of nest relocation in ants remains fairly superficial, and often arises from inferring movements from chance observations of relocated colonies. Only frequent and prolonged monitoring of ant colonies can produce a complete picture of nest relocation behavior. In this study, we document the relocations of colonies of the slavemakers *F. subintegra* and *F. pergandei* over five summers of monitoring raids inflicted on their locally abundant host species, *Formica glacialis*. We investigate the dynamics of these movements, including the roles that slavemakers and slaves play in the process, the distance of the moves, and the timing and duration of relocation. We hypothesize that the purpose of nest relocations of slavemaking ant colonies is to gain access to more raiding opportunities than are available in their current neighborhood where they may have depleted the local supply of hosts to exploit. If slavemakers are relocating nests to achieve higher raiding success, we predict the following:

1. Slavemaker nest relocations should take place in the midst of the raiding season, rather than at the end, and be followed by continued raiding activity (otherwise such relocations could be construed as seasonal migrations to a winter nest).
2. Slavemaker relocation distances should exceed their mean raiding distance before the move if they are motivated to find new raiding opportunities.
3. Slavemaking ant colonies should exhibit shorter raiding distances after relocation than before the move, if they do indeed relocate to areas with higher host density.
4. As slavemaking ant colonies exploit the most convenient targets, raid distances from a given slavemaking ant nest should increase over time.
5. Slavemaker colonies should relocate to areas with higher active host densities than the area they vacate.

Methods

Study site

The colony movements of the slavemakers *F. subintegra* and *F. pergandei* were monitored in the 8-hectare Spencer J. Roemer Arboretum on the campus of SUNY Geneseo in Geneseo, NY. This site consists of secondary successional forest abandoned from pasture about 50 years ago, surrounded by managed lawn and with several canopy openings supporting typical old field vegetation.

Study species

The two slavemaking ants, *F. subintegra* and *F. pergandei*, are members of the *sanguinea* group of *Formica*, which includes 12 species, 11 of which are found in North America (Snelling and Buren, 1985). The best-studied member of this group, the European slavemaking ant, *F. sanguinea*, is a facultative slavemaker, with slavemaking workers participating in all colony activities, including brood care, nest maintenance, and foraging (Hölldobler and Wilson, 1990; Mori et al., 2000). The North American species are less well studied, but were thought to be facultative slavemakers also (Wheeler, 1910). *F. subintegra*, however, exhibits behaviors suggesting that it is an obligate slavemaker: (a) colonies were found to contain invariably 70–90 % slaves (Savolainen and Deslippe, 1996); (b) *F. subintegra* is not active outside the nest until raiding activity begins in July, (c) its slaves are entirely responsible for foraging (Savolainen and Deslippe, 2001). Little information exists about the less common slavemaker in our study site, *F. pergandei*, but it also acts like an obligate slavemaker. It shares with *F. subintegra* the feature of an enlarged Dufour's gland which

produces volatile “propaganda substances” that are sprayed in raids and induce panic in the invaded host colonies (Regnier and Wilson, 1971), whereas the facultative slavemakers *F. subnuda* and *F. rubicunda*, have small Dufour's glands (Savolainen and Deslippe, 1996). Moreover, *F. pergandei* colonies were found to contain slaves in proportions of 58–79 % of the workers (Savolainen and Deslippe, 1996). We observed little slavemaker activity outside of the raiding season and all our focal colonies contained slaves.

Host species exploited by *F. subintegra* include members of the *fusca* group of *Formica*, while *F. pergandei* can exploit members of the *fusca*, *pallidefulva*, *microgyna*, *neogagates*, and *rufa* groups (Fisher and Cover, 2007). In our field site both species only exploit the *fusca* group species *F. glacialis*. *F. glacialis* generally constructs domed nests from excavated earth that can be covered with loose grass and often include a layer of thatch made of leaf and grass fragments (Wheeler, 1908). Its nests can also be more cryptic: under logs, stumps, rocks, or even in mowed lawns. Slavemaker nests assume the same morphology as their hosts. The mean (\pm SD) length, width, and height of slavemaker nest mounds in 2013 were 59.7 ± 11.3 , 61.2 ± 15.3 , and 21.8 ± 8.7 cm, respectively. Based on the literature and preliminary data, mature colony sizes likely number in the thousands of workers. Savolainen and Deslippe (1996) reported colonies of *F. subintegra* ranged from 1,000 to 8,000 in numbers of workers. Analysis of video of raids in summer 2013 revealed that over 2,000 host brood could be retrieved in the most intense 2–4 h of a raid. Raids lasting several days are not uncommon at our field site, although they can also be completed in several hours. Unlike in the facultative *F. sanguinea* (Mori et al., 2000), we have not observed slaves of *F. subintegra* or *F. pergandei* participate in raids.

Field data collection

Since 2008, colonies of these slavemakers' host species, *F. glacialis*, have been mapped using a Trimble ProXH Receiver with Trimble Ranger field computer. We have mapped approximately 800 *F. glacialis* nests in our field site and have located 11 *F. subintegra* and 4 *F. pergandei* slavemaker colonies. Since 2010 we have revisited host nest locations to determine whether the host colonies remain active, based on evidence of recent excavation, response to nest disturbance, or ants visible on the nest surface. Approximately 50–60 % of the mapped nests each year are determined to be active. Inactive nests may be the result of colony mortality, colony relocation, or low activity of the inhabitants at the time of monitoring. Inactive nests may become active again, perhaps through recovery of worker numbers, colony foundation by a new queen, or a relocation event by another host colony. We lack data to distinguish

between the possible processes by which colonies become inactive and active again.

Over the past five summers, we monitored 11–14 slavemaker colonies through repeated daily visits to detect raiding activity and locate host targets. The intensity of monitoring effort differed among years depending on available personnel (2009: 7 July–6 Aug, 31 days; 2010: 15 June–2 Sept, 80 days; 2011: 27 June–19 Aug, 54 days; 2012: 27 June–31 Aug, 66 days, 2013: 26 June–31 Aug, 67 days). In 2009 and 2012, colonies were usually checked at least once daily. In 2010, 2011, and 2013, colonies were typically checked more often, usually 2–3 times daily (except on days of heavy rain). Raiding behavior was identified through observations of slavemakers returning to their home nest with captured brood; raiding trails were tracked to host targets whenever possible, but ability to identify host targets was sometimes hindered by limited time, sparse raiding trails, or vegetative cover. Nest relocation behavior was recognized through observations of slavemakers transporting not only brood but also adult host and slavemaker workers to a new site.

Data analysis

Nest locations were mapped as UTM coordinates. Distances between slavemaker nests and host targets or destinations of moves were calculated in ArcGIS 10. The mean raiding distance before a colony moved was calculated based on all known host targets in the current season prior to a relocation event; in a few cases, we included raids from the end of the previous season if the move occurred early. A Wilcoxon signed ranks test was used to determine if moving distance exceeded the mean raid distance prior to relocation. Spearman's rank correlation was used to examine the relationship between mean raiding distance before a move and the distance a slavemaker moved to a new location. We also compared the raiding distances to targets before and after relocation using a paired *t* test to determine if raiding distances decreased after nest relocation. For slavemaking colonies with at least 10 known raid targets at a single nest location, we tested whether raiding distance increased with time by performing correlations between raid distance and days since the first raid from a site. To compare local host nest densities around vacated slavemaker nests and their destinations after a move we used the “marktable” function of the Spatstat package of R (Baddeley and Turner, 2005). This function allows one to determine the number of features in a given radius around a point. Only nests that had not yet been raided were counted as active host nests on a given move date. We also used the “density” function in Spatstat to generate a kernel density map of active host nests throughout the Arboretum. All statistical analyses, graphs, and maps were generated in R (R Core Team, 2012).

Results

Summary of slavemaker nest relocations

Of 14 slavemaker ant colonies that have been monitored for at least three of five seasons, 13 colonies have relocated at least once in 5 years (Table 1, Fig. 1). Eight colonies moved in more than one season. Six colonies moved two or more times in a single season (mean number of moves per season for mobile colonies = 1.8). Slavemaking colonies always moved into existing host nests; in 27 of 48 individual moves, raids of the destination nest were observed before the relocation.

Timing of relocations

Most colony movements took place between 15 July and 1 August, well after the beginning of the raiding season, which typically starts between 23 June and 1 July (Fig. 2). In at least 18 of the 22 cases of *F. subintegra* colony relocations, the slavemakers continued to conduct raids from their new locations for the duration of the season. For moves of known duration, the average number of days in which ants were engaged in transporting brood and nestmates was 7.11 ± 4.58 (SD). One colony was observed transporting individuals to a new location for a 3-week period. At least three of the six colonies that made multiple moves in a season spent over 3 weeks in colony transport, but they were also engaged in raiding host colonies at the same time from interim locations (Fig. 3).

Raiding distances and nest relocations

Slavemaking ant colonies moved an average of $20.72 \text{ m} \pm 16.10$ (SD) in any single moving event. Cumulative distance traveled by a colony in a season ranged from 3.3 m to 129.5 m [mean = $37.24 \text{ m} \pm 31.77$ (SD)]. The mean distance between a colony's location at the beginning of the season and its final location (total relocation distance) was $29.98 \text{ m} \pm 22.77$ (SD). Mean raiding distances of mobile colonies were calculated before a move and compared to the distance moved to the next location from which they conducted more raids (in some cases they temporarily occupied another nest before moving to a final destination). The distance moved was significantly greater than the mean raid distance prior to initiation of relocation (Wilcoxon signed rank test: $V = 35$, $p < 0.001$; Fig. 4). There was also a significant positive relationship between mean raiding distance and the distance of the move (Spearman's rank correlation: $\rho = 0.6828$, $p < 0.001$; Fig. 5).

The mean distance to targets raided before a move was significantly greater than to colonies raided immediately after a move (paired *t* = 3.545, *df* = 20, $p = 0.002$; Fig. 6).

Table 1 Summary of slavemaking ant colony movements over five seasons

Colony	Species	Total distance moved in meters (number of moves)/Date of beginning of first move				
		2009	2010	2011	2012	2013
4	<i>F. pergandei</i>	0	0	0	0	0
84	<i>F. pergandei</i>	0	0	27.4 (1)/22 July	0	0 ^d
102	<i>F. pergandei</i>	0	0	0	Missing ^b	Missing
416	<i>F. pergandei</i>	— ^c	10.6 (1)/end 2010 ^a	10.6 (1)/June ^a	13.7 (1)/6 July	0
1	<i>F. subintegra</i>	0	0	0	28.7 (1)/22 July	0
7	<i>F. subintegra</i>	20.8 (1)/29 July ^a	81.4 (2)/13 July	76.8 (3)/16 July	80.5 (1)/25 July	30.2 (3) ^e /14 July
11	<i>F. subintegra</i>	16.3 (1)/28 July	35.2 (1)/27 July	0	0	3.3 (1)/June ^a
83	<i>F. subintegra</i>	0	129.5 (6)/27 July	Missing	Missing	Missing
151	<i>F. subintegra</i>	0	4.4 (1)/15 July	0	74.5 (3)/June	39.268 (2)/19 July
177	<i>F. subintegra</i>	0	7.6 (1)/26 July	0	0	0
270	<i>F. subintegra</i>	—	0	0	43.0 (4)/27 June	22.8 (2) ^f /11 July
259	<i>F. subintegra</i>	5.7 (1)/end 2009 ^a	0	62.2 (1)/1 Aug	0	0 ^d
452	<i>F. subintegra</i>	—	—	0	61.7 (3)/17 July	24.9 (2)/30 July
462	<i>F. subintegra</i>	—	—	0	20.1 (1)/19 July	22.5 (2)/14 July

Total distance moved and number of relocations per season. Total distance is the sum of individual moves in a season. Date of first move each season is provided when known

^a Inferred moves (not witnessed directly)

^b Missing: no longer at last observed location; possibly relocated

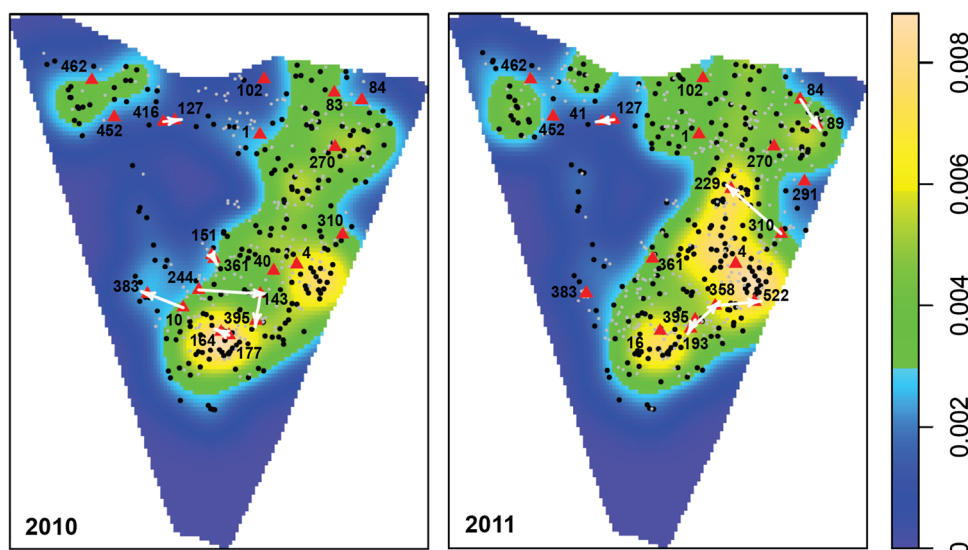
^c Empty cells indicate colonies not yet discovered or tracked during a given year

^d Occupied a second nest location temporarily from which raids were conducted but never vacated original nest

^e Second relocation included two different destination nests

^f Moved back into original nest after raided by another slavemaker and held several interim locations while evading raids

Fig. 1 Map of all observed or inferred slavemaker colony movements in 2010 and 2011. *Solid circles* indicate active (and not yet raided) host colonies. *Gray dots* indicate inactive or raided host colonies. *Red triangles* represent current or previous slavemaker nest locations. *White arrows* indicate directions of slavemaker nest relocations. The map portrays a kernel estimate (with bandwidth sigma = 20) of the average density of host colonies throughout the field site



We also examined the relationship between raiding distance and time using slavemaking ant colonies for which we had a series of at least 10 known host targets from a single location. Of seven slavemaking ant colonies that met this criterion and later moved that same season or relatively early the following season, six showed a significant positive

correlation between days since first raid from a location and raiding distance (Fig. 7). Colony 383, which had a very poor subsequent raiding season with failed relocation attempts, also showed this relationship (Fig. 7). Colony 164, which has remained in the same location since 2010, did not show a trend in raiding distance over time for 2011, 2012, or 2013.

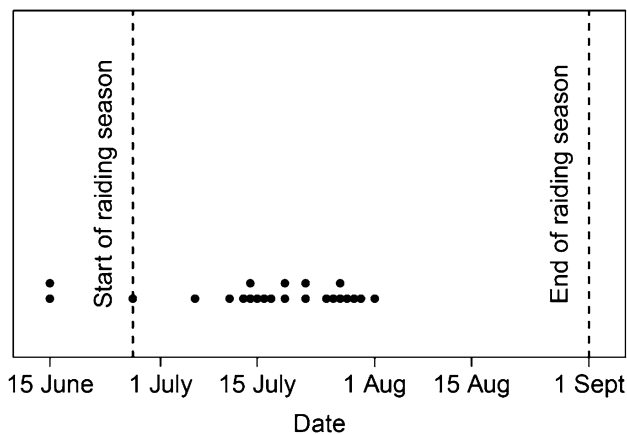


Fig. 2 Dates on which colony movements by slavemakers *F. subintegra* and *F. pergandei* were initiated during 2009–2013. The earliest date on which raids have been documented is 23 June; the raiding season typically ends by early September. Moves represented on June 15 are approximate dates; we know they occurred after the end of the previous year but before the beginning of the raiding season

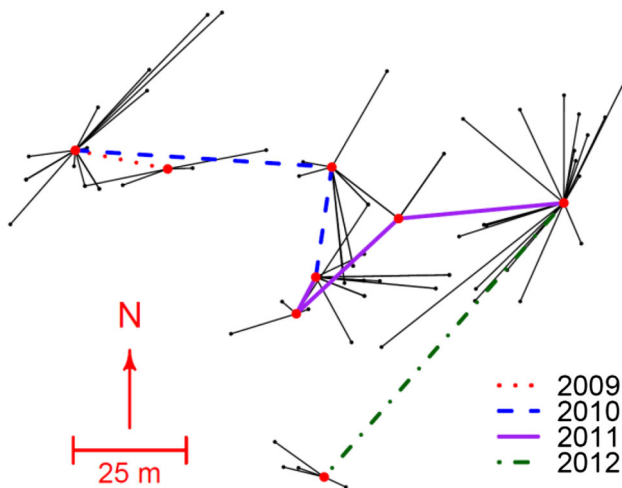


Fig. 3 Raiding and movement history of a *F. subintegra* colony which moved every year 2009–2012. Thin lines indicate raids; thicker lines indicate relocations. This colony relocated once in 2009, twice in 2010, three times in 2011, and once in 2012. It relocated again three times in 2013 (not shown)

Local host nest density

We compared the number of active host colonies within a 10-, 20-, and 30-m radius of vacated slavemaker nest and their new nest locations. In 15 of 18 moves in 2010–2012 of 8 m or longer, the density of active host nests around the destination colony was greater than that around the vacated colony for at least one of the three spatial scales compared (Table 2). Kernel estimates of active host colony density throughout the Arboretum show that slavemaker nest relocations were often directed toward areas of higher host density (Fig. 1).

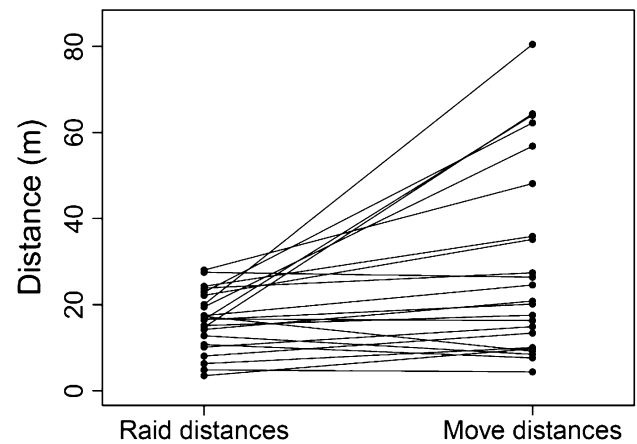


Fig. 4 Mean distances of raids for each mobile colony prior to relocation (or series of movements) and the total actual distance moved from original location. Lines connect these values for each colony/season combination. Colonies which relocated in multiple seasons are represented multiple times in this figure for each substantial move separated by a period of active raiding

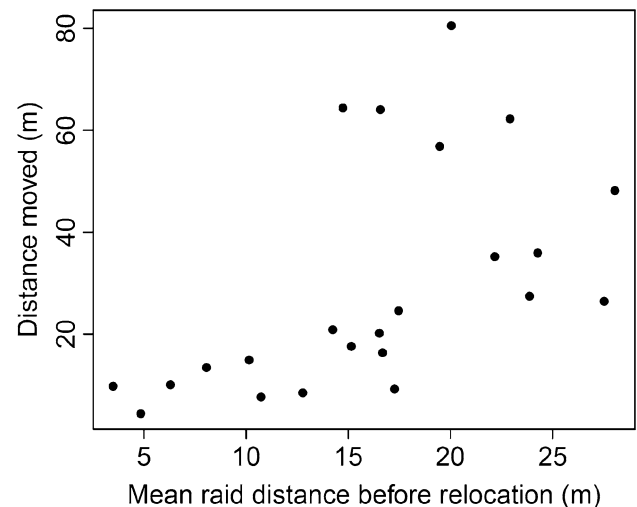


Fig. 5 Relationship between mean distance of raids before relocation and the distance moved to a new nest location

Discussion

Our field study demonstrates that the slavemaking ant species *F. subintegra* and *F. pergandei* regularly relocate their nests. These nest relocations can occur over substantial distances, typically longer than their average raiding distance at their former location. Invariably their new locations are existing host ant colonies which they invade. While nest relocations in ants have a variety of causes (McGlynn, 2012), our data suggest that the most likely purpose of these slavemaker ant movements is to gain access to more host colonies in their new nest site and thus improve their raiding success.

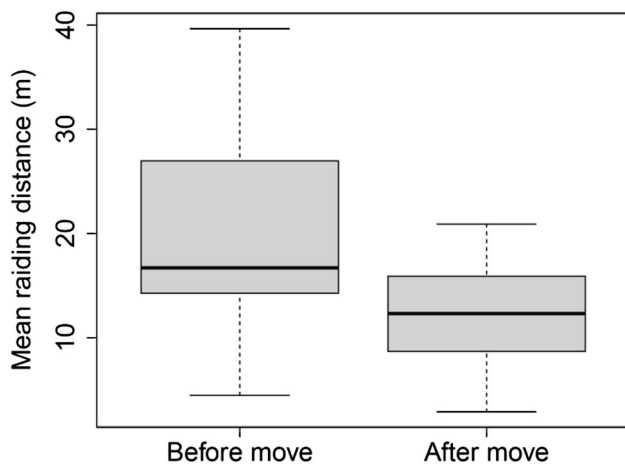


Fig. 6 Mean distance to targeted host colonies before and after a slavemaker nest relocation ($n = 21$ comparisons; for most comparisons a mean of 4–5 colonies was used, depending on availability of data)

Some common reasons for ant nest relocation can be easily ruled out for these species. *F. subintegra* and *F. pergandei* typically occupy large earthen mounds of excavated soil, nest structures that are persistent and stable. Therefore, nest site deterioration is an unlikely reason for their relocations, in contrast to other slavemaking ant species that occupy ephemeral and unstable nest sites like hollow twigs and acorns in the leaf litter (Scharf et al., 2011).

Seasonal migration is documented in a number of ant species. However, the timing of nest relocations in these slavemaking ants suggests they do not represent predictable seasonal movements into sites more conducive to over-

wintering, as has been proposed for other slavemaking species (Wheeler, 1910; Kwait and Topoff, 1983). Movements we observed generally occurred in mid-July while the raiding season was underway but long from concluding. Relocating slavemaking ant colonies usually continued to conduct raids from their new (or interim) locations. If movements represented migration to overwintering sites, we would expect them to occur much later in the season, and we would also expect them to return to a “summer” site at the beginning of the season. However, with few exceptions, slavemakers commence their raiding activity from the nest location we observed at the end of the previous season.

In addition to their timing, the spatial pattern of slave-making ant movements we observed also suggests that relocation is driven by host availability. The distance that mobile slavemaking colonies relocated from their original location at the beginning of the season (either through a single move or several successive moves) generally exceeded the mean distance of raids that they had conducted before moving. This result suggests that slavemaker movements will give them access to host colonies that have not been recently exploited, and thus provide new sources of slaves. Indeed, the mean raiding distance after a move was significantly shorter than before a move, further indicating that the relocation gave slavemakers access to more convenient and numerous host targets. The possibility that slavemaker raids may exhaust local resources is also reinforced by the pattern of increasing raiding distance as the raiding season progresses, particularly observed for those colonies that were soon to relocate (Fig. 7). Slavemaking ant colonies likely exploit the nearest host nests first, and then must venture farther away to find host colonies with

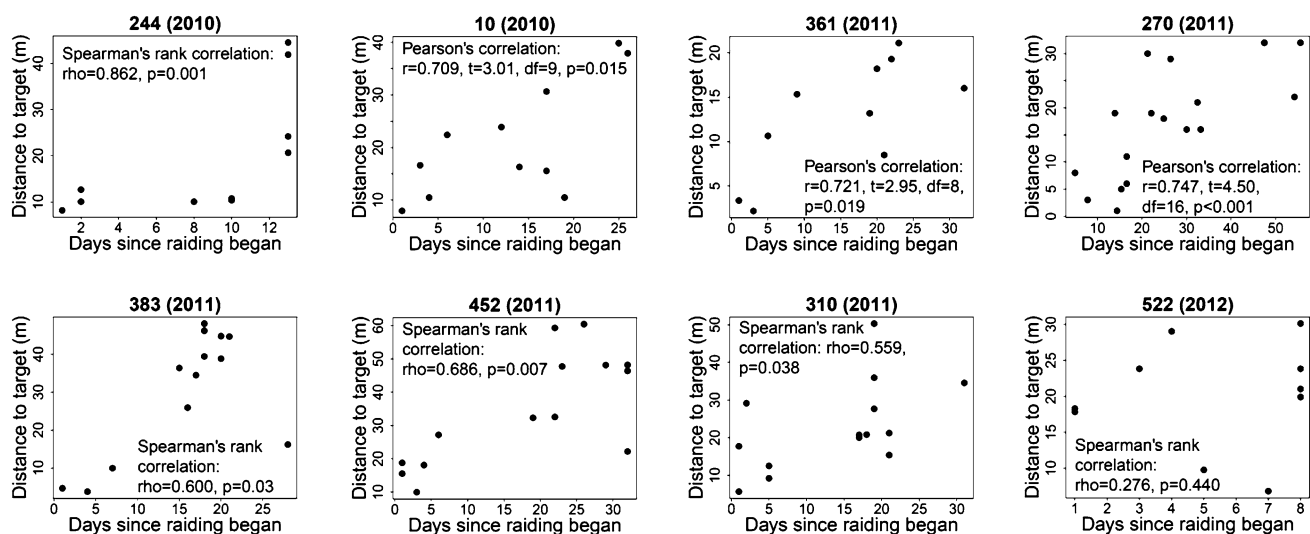


Fig. 7 Relationship between days of raiding and distance to raided target for eight slavemaking ant colonies. Five of these slavemaker colonies moved to a different nest later in the season (244, 10, 361,

310, and 522). Two colonies moved relatively early in the following season (270 and 452). One colony did not move until 2 years later, but had a poor raiding season after the one depicted here (383)

Table 2 Comparison of local host density around vacated and destination slavemaking ant nests

Date	Origin nest	Destination nest	Number of active host colonies						Distance of move (m)
			10-m radius		20-m radius		30-m radius		
			Origin	Destination	Origin	Destination	Origin	Destination	
7-13-10	244	143	1	2	3	7	8	13	56.8
7-31-10	143	395	0	2	3	4	5	14	24.6
7-27-10	10	383	0	5	3	8	10	9	35.2
7-20-11	193	358	0	0	6	9	16	19	30.9
7-23-11	358	522	0	3	8	12	18	22	36.7
7-22-11	85	89	0	2	3	9	12	15	27.4
8-1-11	310	229	1	4	4	15	6	24	62.2
6-15-12	361	632	2	3	7	9	15	18	8.5
7-25-12	632	204	3	0	7	1	16	8	33.0
8-4-12	204	358	0	1	1	12	8	21	33.0
6-27-12	270	266	1	2	3	5	12	12	9.9
7-6-12	266	265	1	1	2	6	9	7	13.0
7-30-12	265	332	0	2	7	5	13	9	14.4
7-17-12	452	603	1	1	4	6	7	9	16.4
7-19-12	462	487	0	1	1	2	8	12	11.7
7-25-12	603	136	1	1	5	7	8	9	16.4
7-22-12	1	502	1	0	7	4	17	7	28.7
7-25-12	522	307	3	3	8	6	18	11	80.5

Number of host nests within a 10-, 20-, and 30-m radius of slavemaking ant colonies. Bold shaded pairs indicate cases in which host density is higher at the destination colony than at the colony vacated during the move. Host nests that were raided before the move date were coded as inactive

brood to raid. Bono et al. (2006b) also found a positive relationship between time and raiding distance in a study of *Polyergus breviceps* and two formicine slavemaking ants. Our estimates of local host nest density indicate that slavemaker colony movements were generally directed toward regions of higher host density than the vacated site (Table 2).

Several authors have suggested the potential for slave-makers to move because of depletion of local host colonies (Wheeler, 1910; Trager and Johnson, 1985; Talbot and Kennedy, 1940); however, such moves have never been investigated in the context of the slavemakers' actual raiding behavior before and after relocation. While the slavemaking ant species we studied generally do not destroy the host colonies that they raid, they may temporarily exhaust nearby sources of host brood over the season. We also found that raided nests are more likely to be labeled as inactive in the subsequent season than nests that are not raided (J. Apple, unpubl. data). This inactive appearance may result from a low level of activity, depleted worker population, nest abandonment, or possibly colony death; we do not have the data to distinguish among these possibilities.

We cannot rule out other reasons for movement, however, such as to relocate to a more favorable microclimate or escape adverse nest conditions like a parasite or disease

(McGlynn, 2012). However, these explanations seem less likely. Relocating to more favorable microclimates would not necessarily require such long moves. The distances moved by these formicine slavemakers (3.2–80.5 m) are higher than relocation distances typically observed for other ant species (Smallwood, 1982a), even large-bodied ants with large nests, like the harvester ant *Pogonomyrmex barbatus* (mean distance = 8.3 ± 1.98 ; Gordon, 1992). Furthermore, in several cases, vacated nests have become reoccupied by host ant colonies, suggesting they are in suitable microenvironments and not contaminated. In fact one nest site that was an interim location for one slavemaker colony on the move became occupied by another slave-maker colony the following year. There are, however, also cases of nest sites that have remained vacant since the departure of their slavemaker occupants.

The mechanics of movements of slavemaking ant colonies that we observed differ strikingly from those described in some other slavemaker species. In *Polyergus lucidus* and *P. breviceps*, nest relocations appear to be largely initiated and carried out by the slaves, which carry adult slavemakers and brood to the new nest location (Marlin, 1971; Kwait and Topoff, 1983; Topoff et al., 1985). Several reports of *Polyergus* workers aiding in the colony movement also exist, though only after the movement was in progress through the

actions of the colony's slaves (Kwait and Topoff, 1983; Trager and Johnson, 1985). In laboratory arenas, the myrmicine slavemaker *Harpagoxenus canadensis* sometimes immigrated into raided host nests; in these movements either or both slavemakers and slaves were observed to initiate and/or participate in the transport of brood and workers (Stuart and Alloway, 1982). In contrast, moves we observed were almost entirely executed by slavemakers; rarely did we see hosts participate in transport.

Nest relocations can be potentially costly endeavors for ants. Some slavemaking colonies at our site spent a substantial amount of time engaged in relocation, sometimes up to 3 weeks. Time spent moving likely takes time away from raiding as well as poses risks to the colony, as brood and reproductives are exposed during the moving process. Nest relocation has been proposed to be more costly to large colonies with large nests requiring substantial excavation (Smallwood, 1982a); however, these slavemaking ants avoid some of these costs by invading already constructed host nests. In addition, genetic data and direct observations of multiple queens being transported during moves indicate that *F. subintegra* are polygynous in this population (J. Apple, unpubl. data), thus reducing risk in case of disruption of the moving trail. This contrasts with data suggesting monogyny for *F. subintegra* at a Canadian site (Savolainen and Seppä, 1996) and for slavemaker ants in general (D'Ettorre and Heinze, 2001). Polygyny is often associated with limited long-distance dispersal (Sundström et al., 2005). Limits to host availability may contribute to constraints on slavemaker colony foundation and their polygynous structure.

The causes, costs, and benefits of the movements of slavemaking ant colonies deserve more investigation. Their mobility not only contributes to their raiding success, but may also significantly impact the structure of the host population. Because potentially long-lived slavemaking colonies must repeatedly exploit host nests in their immediate surroundings to replenish their labor force, colony movement may be a critical component of the ecology of these social parasites that contributes to the spatiotemporal dynamics of this species interaction.

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