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Original Article

Variation in nest relocation of harvester ants is affected by population density and food abundance

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Movement patterns of animals throughout their habitat depend on the associated costs and benefits, which vary among species and potentially among populations. Here, we compare the nest relocation patterns of seed-harvesting ant colonies between 2 populations in northern and southern California, and over time. Understanding the causes and consequences of nest relocation by harvester ants is particularly important because these ants shape the ecological communities in which they reside. We show that nest relocation is both variable between the 2 populations and consistent within a population over more than a decade. Relocation frequency and distance was greater at the site with lower population density, shorter period of vegetation growth, and slightly higher humidity. Thus, when the benefits associated with finding new resources through nest relocation are high and the costs of desiccation or encountering other colonies during relocation are low, nest relocation becomes a preferable behavioral strategy. These findings may explain site-specific ecological dynamics that emerge from the behavioral rules of an ecosystem engineer.

Key words: harvester ant, migration, population density, relocation, Veromessor andrei.

INTRODUCTION

Animals balance various costs and benefits as they move across their environment. Traditional examples of animal movements include natal dispersal (Clobert 2001; Bowler and Benton 2005), seasonal migration (Cohen 1967; Aidley 1981), and excursions in search for resources (Boinski and Garber 2000). Although ant colonies are often perceived as sessile organisms, colonies of many species of ants relocate among nest sites (Smallwood 1982; McGlynn 2012). Nest relocation is associated with benefits such as obtaining new resources (Dornhaus et al. 2004) and avoiding competition with conspecifics (Brown 1999) or other ant species (Dahbi et al. 2008). Relocations have also been suggested as a means of evading parasites or predators (Gordon 1992; McGlynn et al. 2004) or building immunity by moving into nests with pathogens (Pontieri et al. 2014). These benefits may be outweighed by the costs of relocation which include energetic expenditure (Franks et al. 2003), loss of workers and stored food (Tschinkel 2014), sacrificing potential foraging time

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© The Author 2015. Published by Oxford University Press on behalf of the International Society for Behavioral Ecology. All rights reserved. For permissions, please e-mail: journals.permissions@oup.com (Brown 1999), and the risks of desiccation (Feener and Lighton 1991) and predation (Bonte et al. 2012) during relocation. Because the relationship between the benefits and costs of relocation may vary according to ecological requirements, ant species differ in their relocation patterns (Smallwood 1982). Ecological requirements also differ among populations of the same species, yet nothing is known about differences in natural relocation patterns among populations.

Understanding the causes and consequences of nest relocation by harvester ants is particularly important because these ants shape the ecological communities in which they reside. For example, harvester ants influence the abundance and distribution of plant species through seed dispersal (Hobbs 1985; Brown and Human 1997; Peters et al. 2005) and by changing soil nutrients (Wagner and Jones 2006). In addition, the nests themselves influence soil biota (Wagner et al. 1997) and may provide homes for vertebrates (Scherba 1965; Pisani 2009; Esmaeili and Hemami 2013). Thus, differences among populations in nest relocation patterns may have far reaching effects on the structure of their ecological community. Relocation distances may drive the spatial distribution of vegetation growth and seed dispersal, which could affect fire patterns (Minnich and Chou 1997) and the invasion of exotic plant species (Alba-Lynn and Henk 2010). Thus, examining differences among populations of harvester ants in relocation patterns may shed new light on differences in the dynamics of ecological communities.

Colonies of the true harvester ant, Veromessor andrei (previously Messor andrei [Ward et al. 2014]), relocate among nest sites frequently (Brown 1999; Pinter-Wollman et al. 2012). As colonies relocate among nests, they benefit from the move by increasing their distance from their nearest neighbors, thus evading competition with conspecifics (Brown 1999) with whom fights occur when foraging ants from 2 colonies encounter each other, resulting in time and energy costs (Brown and Gordon 2000). Colonies relocate both into existing nests that they or other colonies have excavated, and into newly excavated nest sites (Brown 1999). New nest sites are often within the foraging area exploited by a colony the day prior to relocation, but relocation itself does not appear to be preceded by significant excavation or exploration activity (Brown 1999), unlike in other harvester ants (e.g., Gordon 1992). The foraging activity of V. andrei influences plant distribution and abundance (Hobbs 1985) and their nest mounds, where the ants discard seed husks and often drop seeds too, support a unique plant composition creating patchy plant communities (Brown and Human 1997; Peters et al. 2005). V. andrei are found throughout California (CA) in grasslands, woodland, and chaparral (AntWeb). Here, we tested whether colonies of V. andrei from 2 populations in CA differ in relocation patterns across space and over time. We examine possible causes that might underlie behavioral differences between these 2 populations. Specifically, we compare weather patterns, vegetation growth, and population density to test if differences in desiccation risk, resource availability, and competition with conspecifics may explain intersite variation in relocation patterns.

METHODS

Study sites

The research was conducted at 2 study sites: 1) Elliot Chaparral Reserve (Elliot), University of California, San Diego, CA (117°5'W, 32°53'N) and 2) Jasper Ridge Biological Preserve (Jasper Ridge), Stanford University, CA (122°12'W, 36°25'N), see Figure 1. Observations began at the start of ant activity after winter: the ant population at Elliot was studied from 1 April 2013 to 31 May 2013. The ant population at Jasper Ridge was studied from March to November in 1994 and April to October in 2010; however, to allow for comparison with Elliot, we restricted our analysis to data from the first 2 months of each of these years (24 March-28 May in 1994 and 13 April-14 June in 2010). At the beginning of each field season. 1-2-m-wide transects were conducted throughout an area of 100×300 m² in Elliot and approximately 1 ha at Jasper Ridge to locate and tag individually all *V. andrei* colonies on the site (Table 1). Colonies were tagged using numbered flags or uniquely color-coded bamboo sticks at their nest sites. The plant community was chaparral at Elliot and serpentine grassland at Jasper Ridge.

Colony relocation

To examine colony relocation, we monitored the location of all active colonies 2–3 times a week throughout each field season using a GPS or following the procedure in Brown (1999). A relocation was recorded either if the relocation was observed or if an old and new nest site from consecutive observations could be clearly identified as belonging to 1 colony. Because adjacent colonies rarely relocate simultaneously and all active colonies in the study plots were individually tagged, we were able to determine the identity of most colonies that moved, even when the move itself was not observed. To



Figure 1 A topographical map of California with field site locations.

	Area (m ²) ^a	Number of nests ^b	Number of colonies ^c	Number of colonies/ nest sites	Density of sites ^b (site/ m ²)	Density of colonies ^c (colony/m ²)
Elliot 2013	27159	106	28	0.26	0.004	0.001
Jasper Ridge 2010	10493	31	24	0.77	0.003	0.002
Jasper Ridge 1994	6514	134	60	0.45	0.021	0.009

^aArea (in meter square) of the minimum convex polygon that encapsulates all sites that were active during the field season (see Figure 5).

^bAll nest sites that were occupied during the study period.

Numbers of colonies and nests for each population

^cNumber of active colonies during the study period.

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compare relocation frequency among populations, we counted the number of relocations of each colony, the number of nest sites it occupied, and the number of relocations per nest site to determine if the frequency of moving back and forth between nests differed among populations. To compare relocation distances, we calculated the Euclidian distance a colony moved during each relocation.

Environmental features

To determine the influence of environmental features on relocation frequency, we obtained weather data (mean daily temperature and humidity) from http://www.wunderground.com/ and Normalized Difference Vegetation Index (NDVI) data from http://maps.wfas.net/. The weather station at the Miramar airport (KNKX) was used for Elliot, the station at Central Portola Valley (KCAPORTO4) was used for Jasper Ridge in 2010, and the station in Palo Alto (KPAO) for 1994. Different weather stations were used for the 2 studies at Jasper Ridge because the Central Portola Valley station was not yet active in 1994 and the Palo Alto station provided only partial data for 2010. These stations are in close proximity and produce similar weather data.

Statistics

Table 1

All comparisons among populations of relocations, weather, and nearest neighbor distances were conducted using a 1-way Anova and post hoc Tukey tests. We conducted 8 comparisons among population using Anova; therefore, after adjustment for multiple testing using a Bonferroni correction, Anova P values smaller than 0.006 were deemed statistically significant. The relationship between number of relocations and temperature or humidity was examined using a Pearson's correlation. Because most nest relocations were inferred and not observed directly, we used the average temperature or humidity during the days that elapsed between 2 observations in which a colony was seen at different nest sites as the weather during the relocation.

RESULTS

Colonies of *V. andrei* at Elliot relocated more frequently and to longer distances than colonies at Jasper Ridge in both 1994 and 2010. However, no difference was found in relocation frequency or distance in Jasper Ridge between 1994 and 2010. Colonies at Elliot moved twice as far as colonies in Jasper Ridge (Anova: $F_{2,61} = 13.93$, P < 0.0001; Figure 2a), and the number of relocations observed for each colony at Elliot was significantly greater than at Jasper Ridge (Anova: $F_{2,149} = 48.12$, P < 0.0001; Figure 2b). Each colony occupied significantly more unique nests at Elliot than at Jasper Ridge (Anova: $F_{2,149} = 56.2$, P < 0.0001; Figure 2c). Furthermore, colonies at Elliot were more likely than colonies at Jasper Ridge to move into nest sites they had already occupied, as made evident by the significantly higher ratio between the number of relocations of a colony and the number of nest sites it occupied at Elliot compared with Jasper Ridge (Anova: $F_{2,149} = 23.4$, P < 0.0001; Figure 2d). Still, reoccupancy rates were very low at all sites (medians and upper quartiles are below 1 in Figure 2d).

Although average daily temperature differed between Elliot and Jasper Ridge, we did not find a significant relationship between the number of relocations on a given day and its average temperature. We did not detect a significant correlation between the number of relocations and average daily temperature when considering all sites together (Pearson's correlation: r = 0.26, P = 0.06; Figure 3a) or separately (Pearson's correlation: Elliot: r = 0.18, P = 0.38; Jasper Ridge 2010 [entire season {spring-fall} because of small number of relocations in spring only]: r = 0.01, P = 0.95; Jasper Ridge 1994: r = -0.17, P = 0.47). However, the daily temperature at Elliot was significantly higher than the temperature at Jasper Ridge in both 1994 and 2010 (Anova: $F_{2,175} = 23.46$, P < 0.0001; Figure 3c). In contrast, we observed more relocations on days with higher humidity when data from all sites was pooled (Pearson's correlation: r = 0.35, P = 0.008; Figure 3b) and within each site (Pearson's correlation: Elliot: r = 0.36, P = 0.08; Jasper Ridge 2010 [entire season {springfall} because of small number of relocations in spring only]: r = 0.3, P = 0.05; Jasper Ridge 1994: r = 0.47, P = 0.03). However, Jasper Ridge was less humid than Elliot only in 2010 and not in 1994 (Anova: $F_{2,167} = 7.99$, P = 0.0005; Figure 3d).

The concentration of green leaf vegetation, obtained from NDVI data, was higher at Jasper Ridge in 2010 than in Elliot in 2013 (Figure 4). We were unable to obtain NDVI data for 1994. Furthermore, vegetation remained green throughout the study in Jasper Ridge (Figure 4a–c) but dried up quickly at Elliot (Figures 4d–f).

Not only did the 2 field sites differ in population density, there were also differences in population density between the 1994 and 2010 studies at Jasper ridge. Both nest site and colony density were greatest at Jasper Ridge in 1994 (Table 1, Figure 5). Furthermore, the distance of each colony to its nearest neighbor was significantly longest at Elliot and shortest at Jasper Ridge in 1994, on any given day (Anova: $F_{2,58} = 370$, P < 0.0001; Figure 6a), and for each colony throughout the study (Anova: $F_{2,144} = 33.71$, P = 0.0005; Figure 6b).

DISCUSSION

Ant populations of *V andrei* from 2 different environments exhibited significantly different relocation patterns, but within 1 site, these patterns were highly consistent between 2 periods of observation 16 years apart. Differences in relocation behavior may be driven by population density, with higher density resulting in shorter, less frequent relocations; resource availability, with lower resources driving longer, more frequent relocations; or humidity, where higher humidity may reduce costs of relocation.



Differences between populations in relocation. Average distance that colonies moved (a), number of relocations (b), number of nest sites each colony occupied (c), and moves per nest site (d) differed among study sites. In this and all following boxplots, different letters indicate significant differences using a post hoc Tukey test (P < 0.05); boxes indicate the lower and upper quartiles, horizontal lines within boxes indicate the median, whiskers extend to the 1.5 interquartile range from the box, and open circles indicate outliers.

Competition with conspecifics may cause colonies to escape densely populated areas. Indeed V. andrei colonies at Jasper Ridge tend to increase the distance to their nearest neighbor when they relocate to a new nest (Brown 1999). However, the efficacy of relocating to avoid local competition with conspecifics would increase as population density decreases because the likelihood of encountering another colony during or after a relocation would be smaller in sparse populations than in dense ones. Colonies at Elliot are much sparser than at Jasper Ridge (Table 1, Figure 5); thus, it is possible that because colonies are farther apart from one another at Elliot, relocating to escape local competition is not impeded by high colony densities. According to this, the difference in population density between 1994 and 2010 at Jasper Ridge (Figure 6) would predict more frequent relocations in 2010 when the population was sparser than in 1994. Indeed, when comparing the average number of times colonies relocated among nest sites during the entire season (from April to October), colonies relocated more frequently $(\overline{X} \pm \sigma = 2.78 \pm 2.34)$ in 2010 (Pinter-Wollman et al. 2012) than in 1994 ($\overline{X} \pm \sigma = 0.65 \pm 1.29$) (Brown 1999) (*t*-test: $T_{28.32} = 4.62$, P < 0.0001). The reduction in population density at Jasper Ridge over the 16 years between observations (Table 1) may be explained by competition leading colonies to move apart from one another over time. Nevertheless, there is little direct evidence that competition drives relocations in social insects (McGlynn 2012) and if competition was the sole driver of relocation in this species, one might expect more relocations in denser populations where the potential for competition is greater if resource availability and other ecological variables were equal.

Resource acquisition is an important driver of animal movements. Vegetation was denser and persisted for longer at Jasper Ridge compared with Elliot (Figure 4). Thus, while seeds, which are the primary food of harvester ants, do not limit colony activity in the spring at Jasper Ridge (Brown and Gordon 2000), they may at Elliot. Most foraging activity of V. andrei colonies takes place within 5 m of the nest (Brown and Gordon 2000). The colonies that relocated at Jasper Ridge moved on average 4.93 m in 1994 and 5.17 m in 2010, whereas colonies at Elliot relocated on average distances of 10.58 m (Figure 2a), likely allowing them to explore foraging areas they have not utilized previously. Thus, nest relocation may effectively reduce the environmental variability an ant colony experiences throughout its lifetime because as colonies relocate they resample their environment. Theoretical models predict that dispersal will evolve where resource availability is highly variable in space and time (Roff 1975; Mcpeek and Holt 1992). Indeed,



Effects of weather on relocation. Number of relocations did not significantly increase with temperature (a) but did with humidity (b) when data for all samples was considered (Elliot 2013—white, Jasper Ridge 2010—gray, and Jasper Ridge 1994—black). Temperature differed significantly between the 2 sites (c), but humidity did not (d).

arthropod species that occupy dynamic environments are more likely than species from stable environments to exhibit dispersal or migratory behavior (Southwood 1962). Our results suggest that just as species differ in their propensity to sample their environment by moving in response to resource dynamics, so do populations.

Resource distribution often changes across large geographical scales, leading to behavioral differences among populations. A study of *Temnothorax rugatulus* ants across a large latitudinal gradient found that colonies at higher latitudes are bolder and more active than colonies at lower latitudes (Bengston and Dornhaus 2014). Although our study shows the reverse geographical pattern, that is, the southern population is more active in nest relocation than the northern populations might be similar for these 2 ant species. The northern *T. rugatulus* colonies experience persistent snow pack that shortens their activity season and denser populations which increases their competition over nest sites (Bengston and Dornhaus

2015), thus promoting risk-taking behavior to acquire resources rapidly. Similarly, the southern population of *V. andrei* experiences a shorter period of primary productivity of the plant community in which it resides (Figure 4); thus, the season during which seeds are available is likely shorter than that of the northern population, promoting behavior that maximizes seed acquisition.

The benefits of relocation must be weighed against its costs. Relocation may be risky (Franks et al. 2003) and energetically taxing, for example, because days spent relocating are also lost foraging days (Brown 1999). Thus, frequent relocations to gain access to new resources would be beneficial when competition with other colonies is low and the likelihood of finding habitat that has not been depleted is high, that is, the benefits of arriving at a new location likely outweigh relocation costs. Thus, at Jasper Ridge, where 1) resources are abundant, 2) relocations do not necessarily provide access to new food, and 3) populations are dense, it is possible that relocations are constrained by the high density of colonies (Brown



NDVI data. During the beginning (a, d), middle (b, e), and end (c, f) of the 2010 field season in Jasper Ridge (a–c) and 2013 in Elliot (d–f). Black squares indicate the approximate location of the field sites. Data were obtained from http://maps.wfas.net/.



Figure 5

Locations of nest sites. Maps of all nests that were occupied during the field season at Elliot in 2013 (a), Jasper Ridge in 2010 (b), and Jasper Ridge in 1994 (c). Lines represent the minimum convex polygons that encapsulate all nest sites for each population and were used to calculate area in Table 1. Axes are given in meters.

1999). However, at Elliot, where plant cover and population density are sparse, food may be a limiting factor that triggers frequent and more distant relocations that allow the exploitation of new resources, with minimal costs of encountering new colonies.

In addition to the frequency of relocation, the decision of when to relocate is likely influenced by costs associated with nest relocation. We found a significant positive relationship between humidity and number of relocations (Figure 3b), just as foraging activity increases with humidity in these (Pinter-Wollman et al. 2012), and other harvester ants (Gordon et al. 2013), but in contrast with relocation behavior of other ant species which decreases with humidity (McGlynn et al. 2004). The positive relationship we found between humidity and relocation behavior suggests that colonies choose to relocate when the costs of desiccation are lower. However, because humidity at Elliot was only slightly higher than at Jasper Ridge in 2010 but not different from the humidity in 1994 (Figure 3d), humidity does not appear to explain all the differences in relocation patterns between the 2 sites.

We have shown that nest relocation of seed-harvesting ants, a behavior with important consequences to the ants and their ecological community, is both variable between 2 populations and consistent within 1 population 16 years apart and that these patterns relate to population density, food availability, and possibly to humidity. Further studies are needed across multiple sites that incorporate experimental manipulations to tease these causal factors apart. Harvester ants play a keystone role within their ecological communities (Brown et al. 1979; Davidson et al. 1985; Risch and Carroll 1986; Beattie 1989; Brown and Human 1997),



Differences between populations in nearest neighbor distance. The nearest neighbor distance on any given day (a) and for each colony throughout the study period (b) differed among study sites.

and consequently our findings may explain site-specific ecological dynamics that determine the robustness of the ecological community to perturbations.

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