

Hiking Trails Increase Abundance of Harvester Ant¹ Nests at Clear Creek, Arizona

Derek A. Uhey^{2*}, George C. Cummins³, Michael C. Rotter⁴, Linda S. Lassiter⁵, and Thomas G. Whitham⁶

Abstract. Anthropogenic changes to the environment can sometimes unintentionally benefit ants (Hymenoptera: Formicidae) when habitats are made favorable for nesting. We examined the effects of a hiking trail on nest abundance of *Pogonomyrmex barbatus* (Smith) and *Novomessor cockerelli* (André) harvester ants at Clear Creek, AZ. Nest abundance for both species was compared along paired transects on- and off-trail. *P. barbatus* was twice as abundant on-trail while *N. cockerelli* showed a similar directional trend, but the differences were not significant. To test potential mechanisms driving the increase on-trails, soil and habitat differences were compared. Soil compaction was two times greater and canopy cover was five times less on- versus off-trails. For *P. barbatus*, which nests in soil, we compared on- and off-nest soils, both on- and off-trail. Soil 5 m away from ant nests was twice as compacted whether on- or off-trail. Reduction of canopy cover and compaction of soils might create beneficial nesting conditions for the two species of ant, leading to greater abundance near the hiking trail. Increase of stinging insects near recreational trails might pose health risks, especially in remote areas distant from medical treatment. We discuss management considerations and potential ecological consequences of increased abundance of ants along trails.

Introduction

Anthropogenic changes to the environment sometimes are unintentionally beneficial to insects. Ants (Hymenoptera: Formicidae) commonly take advantage of habitats altered by humans, which can offer improved nesting conditions and increase abundance in colonies of certain species (Menke et al. 2011). For example, colonies along road-sides can be increased for several species including *Pogonomyrmex occidentalis* (Cresson) (DeMers 1993, Terranella et al. 1999), *Messor semirufus* (André) (Itzhak 2008), *Atta laevigata* (Smith) (Vasconcelos et al.

¹Hymenoptera: Formicidae

²School of Forestry, Northern Arizona University, 200 E. Pine Knoll Dr., Flagstaff, AZ 86011

³Department of Biological Sciences, Northern Arizona University, Flagstaff, AZ 86001; Current affiliation: SWCA Environmental Consultants, Flagstaff, AZ 86001

⁴Department of Biological Sciences, College of the Environment, Forestry, and Natural Sciences, Northern Arizona University, Flagstaff, AZ 86011; Current affiliation: Department of Biology, Utah Valley University, Orem, UT 84601

⁵Department of Biological Sciences, College of the Environment, Forestry, and Natural Sciences, Northern Arizona University, Flagstaff, AZ 86011

⁶Department of Biological Sciences and the Center for Adaptable Western Landscapes, Northern Arizona University, Flagstaff, AZ 86011

*Corresponding author email address: dau9@nau.edu

2006), and *Solenopsis invicta* Buren and *S. geminata* (Fabricius) (Tschinkel 1988). For some ant species, disturbed road-side habitats might increase abundance in colonies by offering bare and compacted soil preferred for queens during colony-founding (Vasconcelos et al. 2006).

Anthropogenic-driven increases in abundance of ant nests probably impact ecosystems in close proximity. Ants are important for the functioning of many ecosystems, providing a variety of services and disservices (Del Toro et al. 2012) with consequences for almost all terrestrial food webs (Folgarait 1998). Ants engineer ecosystems through nest construction, increasing habitat heterogeneity, and affecting the structure of ecological communities (Frouz and Jilková 2008, Ellison 2012). Further, increases in ant populations can alter ecosystems through changes to processes such as invasion dynamics (Briggs and Redak 2016), nutrient cycling (Del Toro et al. 2012), and regulation of trophic levels (McNatty et al. 2009).

In particular, harvester ants greatly affect soils and ecological communities by engineering nests and harvesting seeds (MacMahon et al. 2000). Plant communities can be altered to either favor native (Briggs and Redak 2016) or non-native (Paolini et al. 2020) species. Two species of harvester ants, *Pogonomyrmex barbatus* (Smith) and *Novomessor cockerelli* (André), commonly co-occur in many areas of the southwestern United States where they construct large, easily identifiable nests (Fig. 1, MacKay and MacKay 2002). *Novomessor cockerelli* nests usually are under and among boulder-sized rocks, while most *P. barbatus* nests are tunneled into exposed surfaces lacking cover (MacKay and MacKay 2002). Hiking trails are linear disturbances that reduce vegetation cover and compact soils which might increase nest-densities near trails. If so, land management decisions on location of trails might influence abundance of ant nests that in turn influence correlated ecological factors.

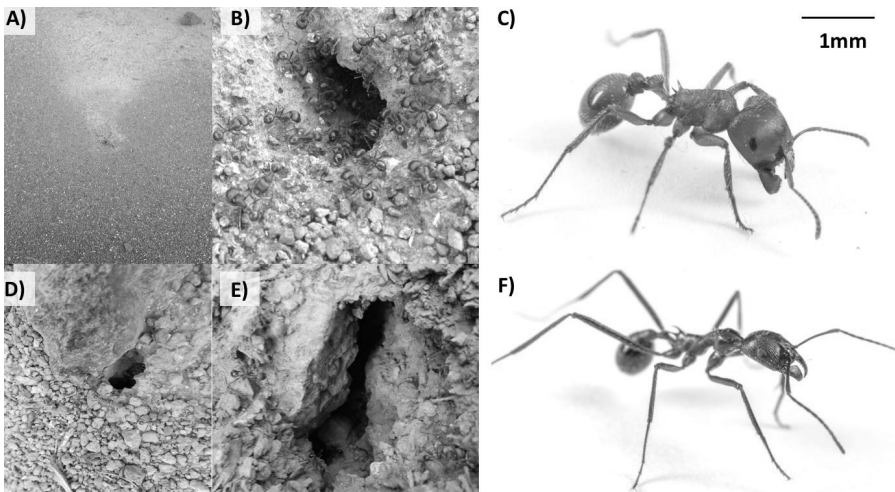


Fig. 1. Harvester ants of West Clear Creek Trail. A) *Pogonomyrmex barbatus* nest, B) close-up of *P. barbatus* nest entry, C) *P. barbatus* worker, D) *Novomessor cockerelli* nest, E) close up of *N. cockerelli* nest entry, C) *N. cockerelli* worker. Scale bar for images C and F.

Whether harvester ant nests were more abundant near West Clear Creek trail and potential mechanisms (i.e., trail changes to canopy cover, ground cover, and soil texture) affecting the patterns were studied. For *P. barbatus*, we also investigated how nesting affected soil (i.e., compaction, pH, moisture, and composition).

Materials and Methods

The study in October 2014 was north of the Bull Pen Recreation Area in Yavapai County, AZ, part of Coconino National Forest (34°32'10.4"N 111°42'39.6"W, Fig. 2). The area has a history of cattle grazing followed by recreational use by day hikers who use the site as access to nearby West Clear Creek. The average site elevation is approximately 1,100 m and in the Verde River watershed. Our study was done along a recreational hiking trail that follows a wide canyon bottom outside the riparian corridor paralleling West Clear Creek. The single-track trail was formed on a pre-existing forest service road, but has been exclusively foot-trafficked since 1984. The trail cuts through areas of mesquite (*Prosopis juliflora* (Sw.) DC, Fabales: Fabaceae) with intermittent open habitats of mixed species including native grasses (e.g., *Bouteloua eriopoda* (Torr.) Torr. and *Aristida arizonica* Vasey, Poales: Poaceae), shrubs (e.g., *Artemisia ludoviciana* Nutt., Asterales: Asteraceae), cacti (e.g., *Opuntia macrohiza* Engelman, *O. engelmannii* Salm-Dyck ex Engelman, and *Cylindropuntia acanthocarpa* Engelman & J.M. Bigelow, Caryophyllales: Cactaceae), and exotic red brome (*Bromus rubens* L. Poales: Poaceae).

To determine abundance of *P. barbatus* and *N. cockerelli* on- and off-trails, ant nests were counted along three paired 200 x 6-m transects. For each pair, one transect was along the trail (encompassing both trail and trail-side habitats), and the other 20 m away and parallel to the trail. Each transect encompassed suitable habitats for both species (i.e., areas with boulders for *N. cockerelli* and barren surfaces for *P. barbatus*).

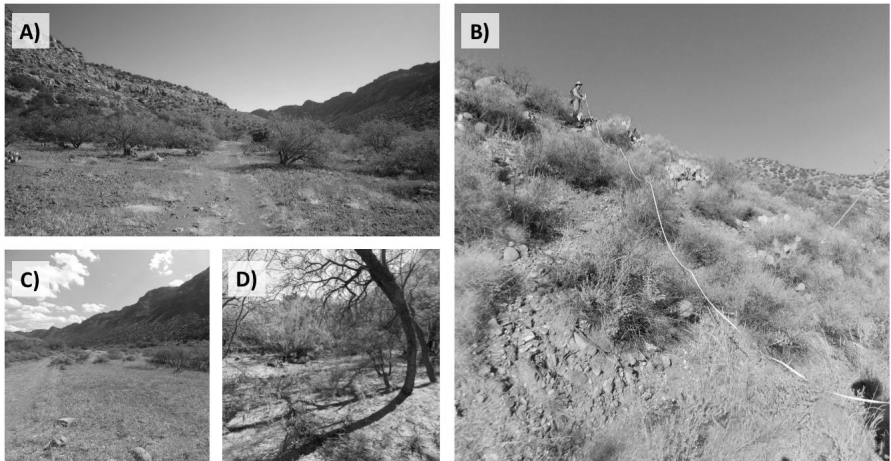


Fig. 2. Study location at West Clear Creek Trail, Coconino County, AZ. A) Mixed-mesquite and grassland habitat on-trail, B) mixed shrub-cactus habitat off-trail, C) open grass-dominated habitats on- and off-trail, and D) mesquite-dominated habitat with canopy off-trail.

To test possible mechanisms influencing abundance of ant nests, habitat characteristics were compared between on- and off-trail transects. Along each transect, canopy cover, ground cover, and soil infiltration rate were estimated every 20 m on both edges of each transect ($n = 20$ per transect). Canopy cover was measured by looking straight up through a 2.5-cm-diameter circle held at eye level (approximately 1.75 m above the ground). Ground cover was measured within a 1-m² quadrat documented by functional group (i.e., grass, forb, shrub, or tree). Soil infiltration rate was measured *in-situ* as the infiltration rate for dry soil, litter removed, and converted to milliliters per hour. Low infiltration values indicated very compacted soil, and vice versa.

To test how *P. barbatus* nests modified soil, several standard soil tests were measured at two randomly selected *P. barbatus* nests per transect ($n = 2$ per transect) and paired with off-nest areas 5 m away but still either on- or off-trail ($n = 2$ per transect). *N. cockerelli* were unable to be tested for soil effects, because their nests are built among boulders. At each location, infiltration rate and soil composition were measured (methods from USDA 2001). The infiltration test involved pouring 444 ml of tap water in a 15.24 cm ring 0.5 cm into the surface soils. The amount of time for the water to penetrate the surface soil layer was recorded in seconds. Soil composition was evaluated using a 15-cm-deep column sample taken 0.5 m (on-nest) and 15 m (off-nest) away from the main nest opening. The composition measurements were moisture content, grain size (i.e., gravel proportion), organic content, and pH. Moisture content was calculated from pre- and post-drying weights of samples heated overnight in a 105°C oven. Gravel proportion of the sample was calculated as the weight of material that did not pass through a 2-mm sieve that was the delimiter dividing gravel from sand-sized particles. The percentage of organic matter was determined using pre- and post-combustion sample weights heated at 600°C for 24 hours. A pH meter was used on diluted samples of two parts tap water to one-part soil.

Data were analyzed using the statistical program Minitab (V.14) and Program R (R Core Team 2020). Normality was tested with Shapiro-Wilk tests and variance homogeneity tested with *F* tests or Levene's tests. Abundance of ant nests and canopy cover were compared between transects with Welch two-sample t-tests, or Wilcoxon rank-sum test if data were not distributed normally. Soil and ground cover variables were analyzed using factorial ANOVAs comparing each variable with the main effect and interaction terms of whether the sample was from an on-/off-trail and on-/off-nest.

Results

Pogonomyrmex barbatus nests were about twice as abundant as *N. cockerelli* nests, and nests of *P. barbatus* were more abundant on trails (Fig. 3). The latter pattern was consistent across all transects through varying habitat types. *Novomessor cockerelli* nests were not significantly different on- and off-trails.

Canopy cover was five times more along off-trail transects compared to those on-trail (Fig. 4). Ground cover metrics showed mixed results, with no significant relationship between vegetative ground cover and areas on or off trail, or at and away from nests. However, approximately eight times more litter ground cover was on compared with off trails ($F_{1,20} = 8.89$, $p = 0.007$) and three times more bare ground off trails compared with on trails ($F_{1,20} = 20.99$, $p < 0.001$).

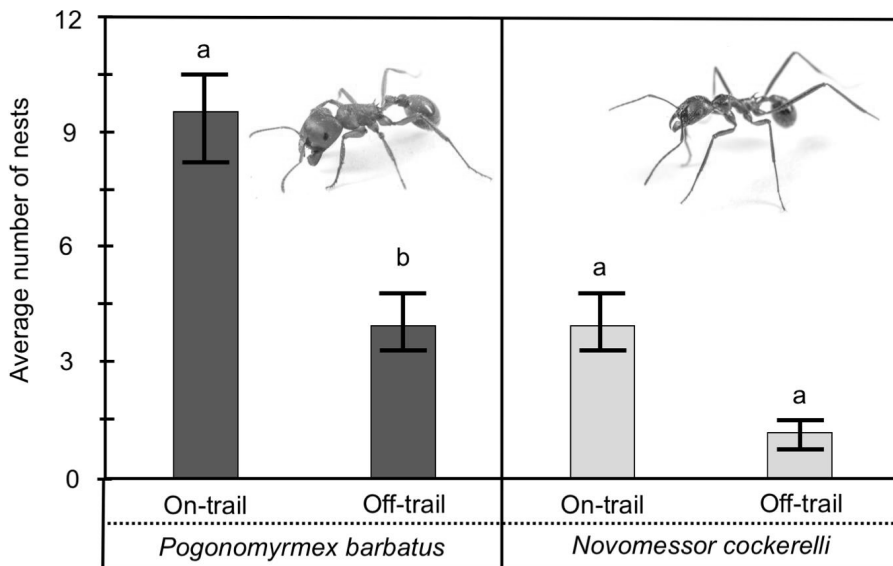


Fig. 3. Number of nests along transects on- and off-trail of two harvester ant species (*P. barbatus*, $t = -2.48$, $p = 0.042$; *N. cockerelli*, $t = -1.977.78$, $p = 0.108$). Vertical bars represent ± 1 SE, and different letters signify significant differences.

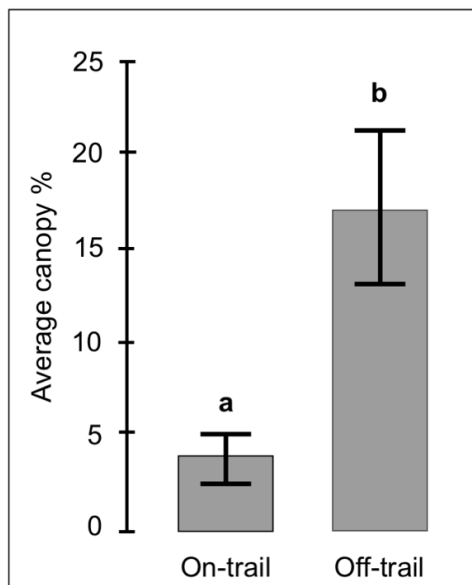


Fig. 4. Significant differences in percentage of canopy cover ($W = 19.87$, $p = 0.002$), B), vertical bars represent ± 1 SE, and different letters signify significant differences.

ANOVA comparing each soil composition variable with the main effects of soil from on-/off-trail and on-/off-nest, along with an interaction term, found no significant differences except in infiltration rates (Table 1). Soils of *P. barbatus* nests had significantly greater infiltration rates (i.e., less compaction, $F_{3,23} = 8.27$, $p = 0.025$) compared with soil 5 m away.

Table 1. Soil Measurement Means \pm SE of *P. barbatus* Nests and 5 m Away, On- and Off-trail

Transect	Moisture %	Gravel %	Organic %	pH	Infiltration (ml/hour)
On-nest					
On-trail	5.2 \pm 1.0	36.4 \pm 6.2	5.3 \pm 0.6	8.2 \pm 0.2	23.4 \pm 2.3*
Off-trail	5.0 \pm 0.3	34.4 \pm 4.7	5.1 \pm 0.3	8.1 \pm 0.1	41.0 \pm 9.2*
Off-nest					
On-trail	4.8 \pm 0.7	28.5 \pm 2.6	6.0 \pm 0.5	8.2 \pm 0.1	15.0 \pm 2.3*
Off-trail	5.0 \pm 0.5	30.1 \pm 6.2	5.5 \pm 0.8	8.2 \pm 0.1	31.3 \pm 2.3*

*significantly different ($\alpha = 0.05$).

Discussion

We found more nests of *P. barbatus* associated with recreational trails. Similar increases are known for *Pogonomyrmex occidentalis* along asphalt roads in North Dakota (DeMers 1993) and trails in Colorado (Terrenella et al. 1999). However, we found no difference on- and off-trail for *N. cockerelli* nests.

Differences in canopy cover, ground cover, and soil compaction on-and off-trail habitats suggested *P. barbatus* might benefit from habitat alterations near trails. DeMers (1993) suggested bare-soil areas near roads resembled nuptial landing sites, encouraging colony founding. While we found more bare ground off-trail, we believe this is a result of canopy shading that discourages harvester ants. Harvester ants prefer to nest in xeric environments (MacMahon et al. 2000), and workers are more common in open (versus canopied) habitats (Uhey et al. 2020a, 2020b). Reductions in woody plant cover are positively correlated to increases in colony densities (Holbrook et al. 2016). Increase in abundance of nests might partly be caused from resulting increase in solar irradiance and temperature of surface soils in areas with less canopy cover, such as we found along the trail.

An unintended consequence of recreational trails in harvester ant habitats can be more nests of harvester ants in areas used by humans. Stings by *Pogonomyrmex* are painful and potent (Schmidt 2019) with a small number of victims hospitalized with anaphylactic shock (Klotz et al. 2005). Increased nests near trails might therefore affect recreation quality and public health. Peak symptoms from a reaction to ant stings typically occur within 30 minutes (Klotz et al. 2009) and many trails, such as West Clear Creek, are more than 30 minutes from medical treatment.

Greater abundance of harvester ants likely alter plant communities near trails through preferential seed-harvesting (MacMahon et al. 2000). Ants either might prefer native seeds thereby reducing competition for exotics (e.g., Schmasow and Robertson 2016), or prefer exotic seeds thereby promoting exotic colonization (e.g., Briggs et al. 2016). Whether harvester ants help or hinder establishment of invasive plant species is context-dependent because, along with other factors, seed-preferences vary among ant species (MacMahon et al. 2000). Preference of *P.*

barbatus for seeds of native or exotic plant species is unknown but might impact invasion ecology near trails.

Harvester ants further affect ecosystems by nesting that creates biodiversity and nutrient hotspots (Wagner and Jones 2004). While soil compaction can pose a problem for ecosystem functions by allowing invasive species to colonize, increasing soil erosion, and disrupting soil food webs (Zaitlin and Hayashi 2012), ant nests reverse soil compaction in their immediate nesting area. We found *P. barbatus* along compacted trails were able to locally reverse impacts of soil compaction through nesting activity. Nests can become islands of fertility (Wagner and Jones 2004) in a compacted soil matrix, facilitating plant growth (Coffin and Lauenroth 1990) and serve as points of recovery for vegetation following disturbance such as drought (Nicolai et al. 2008) or fire (Nicolai 2019). If the same is true for ant nests along recreational trails, this might lead to vegetation recovering more quickly from disturbance in close proximity to trail systems. This also suggests potential for ants to enhance reclamation of abandoned trails and roads, something of concern for local land managers along the Verde watershed (Brock and Green 2003).

Our results highlight how recreational trails can be unintentionally beneficial to harvester ants and suggest this has cascading effects on ecosystems near trails. The effects of harvester ants can be positive or negative depending on the ecological context. It might be important to consider interaction among harvester ants with native and invasive plants for restoration goals or increase in stinging insects for recreation goals, when constructing and managing trails or roads.

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