

Funnels, gas exchange and cliff jumping: natural history of the cliff dwelling ant *Malagidris sofina*

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Abstract The Malagasy endemic ant *Malagidris sofina* (Bolton and Fisher 2014) nests on cliff faces in natural rock alcoves or clay banks. Colonies have single ergatoid queens and reproduce by fission. Each nest has a funnel-shaped entrance that projects horizontally from the cliff face. We examine three hypotheses for the function of the funnels—water exclusion, gas exchange and defense. Entrance funnels are relatively impermeable and divert water from nests, but simple tubes would achieve the same result. Consistent with the gas exchange hypothesis, projected funnel entrances likely increase gas exchange rates over sixfold compared to simple tubes and may increase air flow within the nest. Gas exchange may explain the recurrent evolution of funnel entrances in several ant lineages, especially among cliff dwelling species. We outline *M. sofina* defense responses to conspecifics and co-occurring ant species, and find no support for a defense role of entrance funnels. Workers display little aggression but respond to several species with an original form of nest defense—cliff jumping—in which workers drop off the cliff face while clinging

to invaders and then return to their nest. *M. sofina* is a restricted range species under threat of extinction by habitat destruction. Its novel lifestyle underscores the urgency of exploration and conservation in a tropical biodiversity hotspot.

Keywords Cliff dwelling · Cliff jumping · Madagascar · *Malagidris sofina* · Nest entrance · Nest ventilation

Introduction

Nests are central to social insect life histories, influencing species interactions, the organization of colony labor, and environmental conditions experienced by colonies (Hölldobler and Wilson 1990; Sendova-Franks and Franks 1995; Tschinkel 2004). The ant *Malagidris sofina* (Bolton and Fisher 2014, Fig. 1) (Myrmicinae) of northwest Madagascar commonly nests on cliff faces (Fig. 2). Colonies build nests by deepening natural sandstone alcoves and enclosing them with porous mud walls, or by excavating vertical clay banks. Each nest has a funnel-shaped entrance several centimeters across that projects from the cliff surface (Fig. 3). The function of these conspicuous entrances, however, is unclear.

Funnel entrances have arisen independently in several distantly related ant lineages, and various hypotheses have been proposed for their function. Nests of *Harpegnathos saltator* and *H. venator* in India and Southeast Asia have flanged entrances that may keep predators from the nest (Peeters et al. 1994; Crosland 1995). In Central America, *Stenammas alas* and *S. expositum* have funnel entrances with small openings that may defend against army ants, divert water from the nest, serve as recognition cues for searching males, or disperse colony odors (Longino 2005). Also in

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Fig. 1 *Malagidris sofina* worker (CASENT0003236) (a–c) and ergatoid queen (CASENT0420020) (d) (AntWeb 2014)

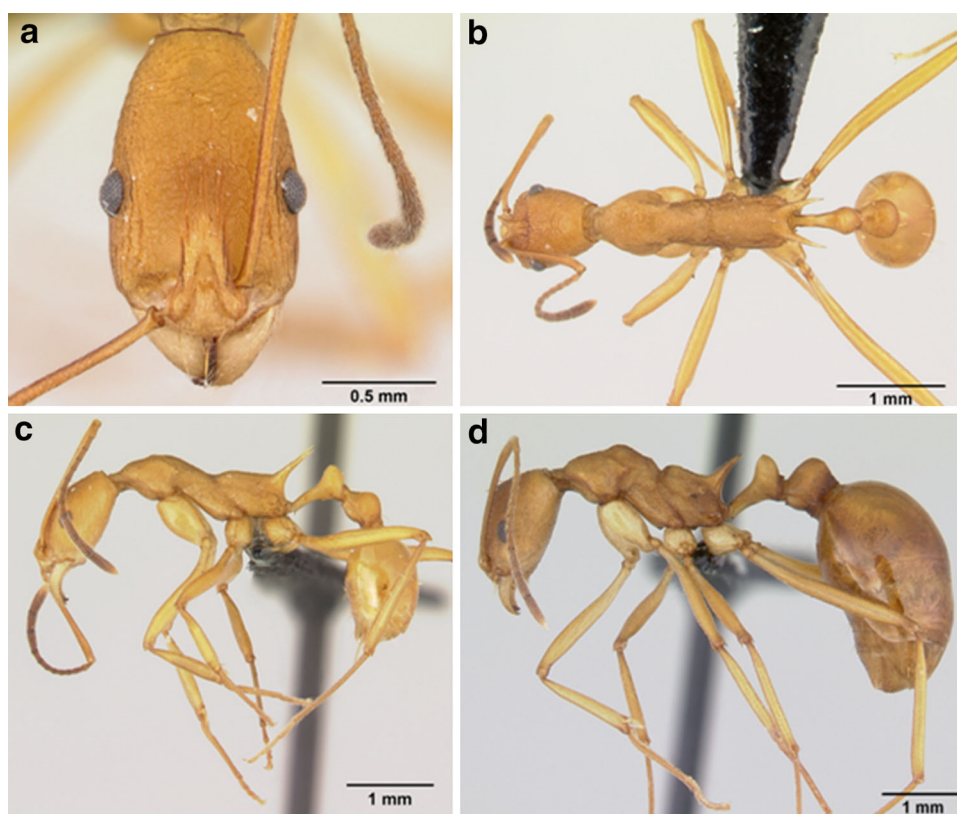
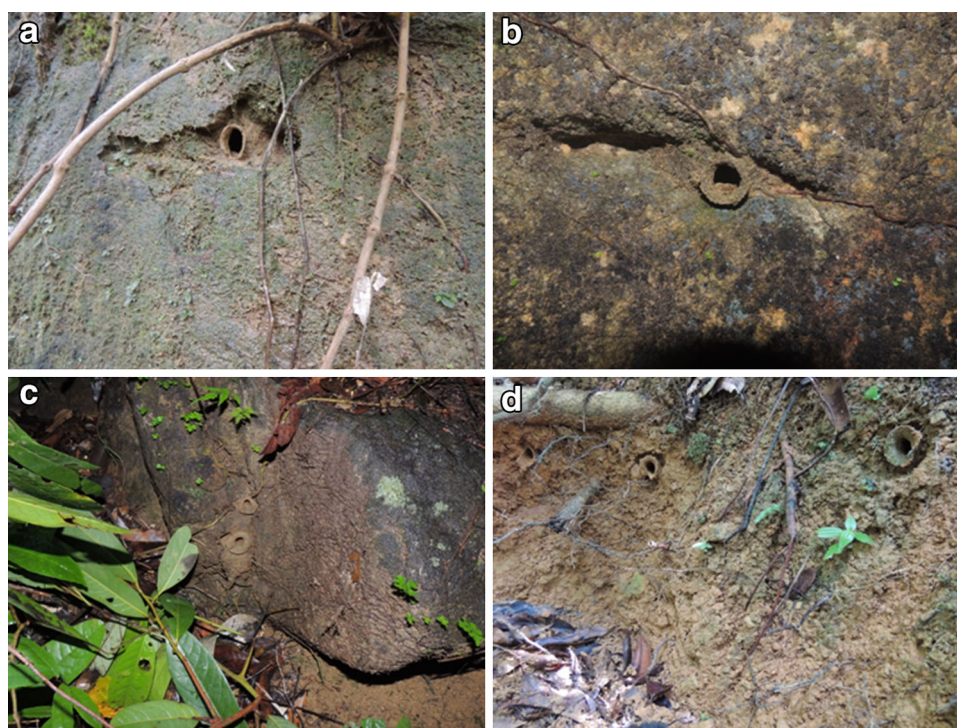


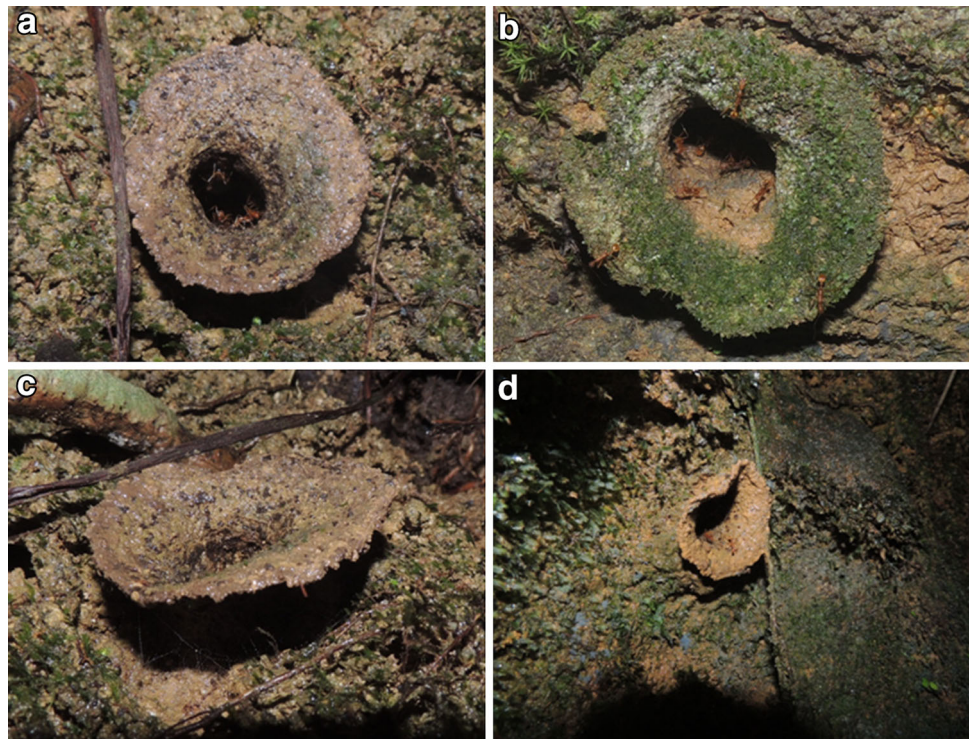
Fig. 2 *Malagidris sofina* nests in cliff alcoves (a, b), cracks in boulders (c) or clay banks (d), and may be polydomous (c, d)



Central America, the fungus gardening ants *Cyphomyrmex longiscapus* and *Trachymyrmex zeteki* build funnel entrances which appear to function neither in water exclusion nor defense (Mueller and Wcislo 1998; Pérez-Ortega et al.

2010). Finally, an undescribed *Lordomyrma* species in Borneo builds funnel entrances of unknown function (B. Fisher, unpublished). All these species, including *M. sofina*, nest in moist or waterlogged substrates, and all but

Fig. 3 *Malagidris sofina* nest entrances in clay (a, c) and rock (b, d)



one are obligate cliff dwellers. The exception, *H. saltator*, lives in flat soil in seasonally flooded monsoon forests. Its nests, however, consist of dense clay spheres built inside excavated cavities and, as in cliff dwellers, are accessed by horizontal nest openings (Peeters et al. 1994). Among the six known *Malagidris* species, *M. sofina* is the only cliff dweller and the only one known to build funnel entrances (Bolton and Fisher 2014). If these convergent nest architectures have an adaptive function, they have thus likely evolved in response to similar ecological conditions associated with cliff dwelling or moist soil. We group the proposed funnel functions into three hypotheses—water exclusion, gas exchange and nest defense—and evaluate them in *M. sofina*.

Rainforest rock faces and banks are often wet and may experience flowing water. The water exclusion hypothesis asserts that *M. sofina* funnel entrances keep nests dry. It assumes that funnel shape and orientation divert water from the nest interior and that the funnel is impermeable. Water exclusion is unlikely for the two species of fungus gardeners as they nest in protected areas under overhangs (Mueller and Wcislo 1998; Pérez-Ortega et al. 2010), and for cliff dwelling species in general, as a simple tube would achieve the same result as a funnel (Longino 2005).

The gas exchange hypothesis asserts that nest entrances create air currents that ventilate the nest, cool the colony or disperse odors. It assumes that diffusion is insufficient for a colony's metabolic or thermal demands, or that dispersing odors aid in defense or mate attraction. Carbon dioxide can build up in ant nests to many times atmospheric levels,

especially in impermeable materials like wet rock or clay (Cox and Blanchard 2000; Kleineidam and Roces 2000). Gas and temperature regulation may be especially difficult in cliff nests with horizontal openings which preclude gas exchange by vertical convection currents. Ants are sensitive to CO₂ concentrations (Kleineidam and Tautz 1996; Kleineidam and Roces 2000) and nest entrance modifications are an effective way to regulate them (Vogel et al. 1973; Vogel 1994; Cox and Blanchard 2000). Ventilation systems are common among termites (Lüscher 1961; Weir 1973), which use air currents as construction cues (Howse 1966), and some leaf cutters (*Atta vollenweideri*) use vertical turrets to facilitate gas exchange (Kleineidam et al. 2001). Projecting entrances increase gas exchange rates by protruding beyond the still boundary layer to faster air currents. Moving air and viscosity may create a pump, drawing air through pores in nest walls and out the entrance. At the same time, widened entrance mouths increase the surface area for gas exchange and the rate of air flow to the nest. A version of this hypothesis was proposed for *Stenamamma* species, where funnel entrances may disperse colony odors and prevent detection by army ants (Longino 2005). Gas exchange is especially relevant for the two fungus gardeners, which have increased colony metabolic rates and stricter thermal demands due to their symbiotic fungi (Mueller and Wcislo 1998; Kleineidam et al. 2001; Pérez-Ortega et al. 2010).

The defense hypothesis asserts that funnels keep enemies—most likely other ants—out of the nest. Defense can involve any of the following mechanisms—the funnel is an

obstacle that impedes entry, is a warning system that alerts the colony to intruders, or provides an advantage in combat and is actively defended. In Meliponini bees funnel-shaped entrances provide fighting platforms for defending workers (Roubik 2006). *Stenammina* species build entrances that are too narrow for army ant entry and block them with pebbles, but in contrast to Meliponines do not actively defend the funnels (Longino 2005). The orientation of *H. venator* funnels may make it difficult for predators to navigate and enter (Crosland 1995). In the fungus gardening species, however, the entrances are too large to prevent predator entry (Mueller and Wcislo 1998; Pérez-Ortega et al. 2010), and in *T. zeteki* have no effect on rates of wasp parasitism (Pérez-Ortega et al. 2010).

These hypotheses are not mutually exclusive and any combination may be at work in *M. sofina*. Further, the funnels may be an artifact of nest construction and have no adaptive value. Under this null hypothesis, entrance funnels may vary with nest substrate or mode of construction, and if destroyed would not be rebuilt. We performed a series of field experiments to evaluate some of the assumptions and predictions of the competing hypotheses. In doing so, we also describe the reproductive ecology and defense behaviors of *M. sofina*. Our results uncover novel behaviors and underscore the urgency of conservation in a tropical biodiversity hotspot.

Materials and methods

We investigated the natural history of *M. sofina* in February 2013 during an expedition to an unprotected primary forest fragment in the Galoko Massif in northwest Madagascar (13°35'6"S, 48°43'5"E, 520 m elevation). Galoko lies in the Sambirano region of seasonal rainforest. Within the Sambirano, *M. sofina* inhabits wet forest below 1,200 m and produces similar nest structures throughout its range. Galoko's remaining forest fragments are largely unexplored and are threatened by increasing pressure from slash and burn agriculture (Callmander et al. 2008, 2009). Our visit represents the first study of the area's ant fauna. Voucher specimens are deposited at the California Academy of Sciences (AntWeb 2014).

Nest description

Nests were patchily distributed on scattered rock outcrops, large boulders, and recently eroded clay banks (Fig. 2). We measured 25 nests, 19 in rock and 6 in clay. Nests consisted of a single chamber with a funnel-shaped entrance that projected horizontally from the cliff face (Fig. 3). Although generally elliptical, funnels were often asymmetrical or

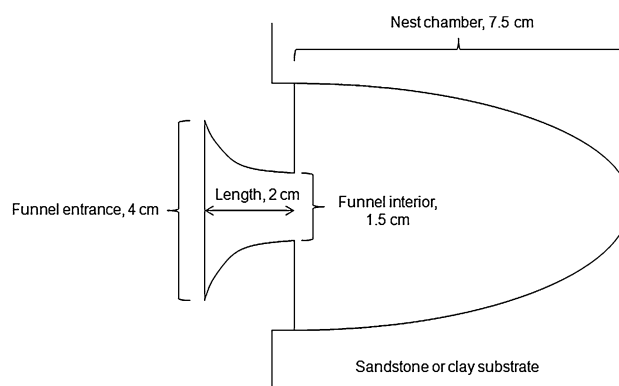


Fig. 4 *Malagidris sofina* nest diagram, drawn to scale with major axes of the funnel entrance and interior

damaged. Rock nests used natural or enlarged alcoves, while clay nests were excavated, sometimes with a depression around the base of the funnel. Alcoves were enclosed with thin mud walls, sometimes laced with hanging roots. Mud walls were often porous and penetrated by holes up to 2–3 mm in diameter. Funnel entrances were made of soil collected inside the nest or carried from the ground below, and sometimes had moss growing on them (Fig. 3b). We measured the dimensions of each nest entrance—major and minor axes of the funnel edge (entrance), major and minor axes of the narrowest part of the funnel (interior), and length of the funnel from interior to entrance (Fig. 4). To further characterize funnel shape, we calculated the cross-sectional areas of the funnel entrances and interiors and the ratio of the two. To see if nest entrances varied with colony size, we compared whether funnel length, entrance area, interior area and area ratio varied with nest depth. Nest depth—from the base of the entrance funnel to the rear wall—was measured by probing the nest with a twig. To see if substrate influenced nest entrance design, we used Kruskal–Wallis tests to examine whether rock and clay nests differed in depth, funnel length and entrance area. We removed four entrance funnels to observe rebuilding behavior and perform water exclusion experiments (see below). Not every nest was measured for every trait, and we note sample size for each analysis. Finally, we collected fifteen live colonies, counted workers, and dissected and checked queens for ovarian development to determine reproductive biology.

Polydomy

Several nests were within 30 cm of each other (Fig. 2c, d), suggesting that colonies use multiple nests. To examine the possibility of polydomy, we transplanted workers from adjacent nests and checked for aggression and whether workers entered other nests. We further observed unmanipu-

lated workers to see if they naturally moved between nests. In two cases, we excavated nests to check for connections beneath the surface.

Water exclusion

We investigated the water exclusion hypothesis in two ways. To see if funnels divert water from nests, we pipetted water onto nests and entrances and observed flow patterns. To examine entrance permeability, we excised two intact funnels. We placed each funnel upright in a plastic container, sealed it to the bottom with candle wax, and filled the container with water to the height of the funnel. We then pipetted medical iodine solution into the water outside the funnel to observe whether it diffused through the funnel wall into the interior. The experiment was repeated for each entrance, the second time pipetting the iodine solution into the funnel interior to see whether it diffused out.

Gas exchange

We investigated the gas exchange hypothesis by examining nest architecture and colony metabolic demands. In general, funnel-shaped entrances are superior to simple tubes for inducing air currents (Vogel et al. 1973; Weir 1973). We investigated two funnel characters that affect ventilation—entrance cross-section and entrance area ratio. Viscosity and low pressure due to higher air speed (Bernoulli's principle) combine to draw air from the entrance at a rate of flow per unit area. The entrance cross-section thus represents the area available for gas exchange and is proportional to the amount of air exchanged through diffusion or pulled through the nest in case of an induced current. Second, the principle of continuity dictates that the amount of air flowing through any point of the funnel is equal, so that air flows faster in the narrow interior than the wide entrance. An entrance with twice the area of the interior would mean air in the interior flows twice as fast. In this way, even low gas exchange rates can create fast air currents in the interior and through pores in nest walls. The ratio of entrance to interior area—how flared the funnel is—indicates relative air speeds.

We also calculated oxygen demands and carbon dioxide production of a colony. We dried six workers for 48 h at 60–65 °C and weighed them with a Cahn microbalance. We calculated average O₂ demand per worker using a formula determined for *Temnothorax unifasciatus*, 0.61 μl O₂ h⁻¹ mg⁻¹ live weight (Martin 1991; Cox and Blanchard 2000), and a live to dry weight ratio of two (Tschinkel 1993). Our estimate was comparable to resting measurements of similarly sized *Solenopsis invicta* (Porter and Tschinkel 1985; Vogt and Appel 1999) and *Leptogenys nitida* (Duncan and Crewe 1993; Lighton and Fielden 1995). To convert O₂ demands to CO₂ production, we used a respiratory quotient

Table 1 Experimental introductions to *Malagidris sofina* nests

| Species | <i>n</i> | Aggression | Drag | Drop |
|-----------------------------|----------|------------|-------|-------|
| <i>Bothroponera</i> sp. | 4 | 0 | NA | NA |
| <i>Camponotus</i> diurnal | 21 | 0.57 | 0.625 | 0.125 |
| <i>Camponotus</i> nocturnal | 10 | 0.80 | 1.00 | 0.50 |
| <i>Cerapachys</i> sp. | 28 | 0.36 | 0.70 | 0.70 |
| <i>Crematogaster</i> sp. | 6 | 0.50 | 0 | 0 |
| <i>Malagidris sofina</i> | 5 | 0 | NA | NA |
| <i>Pheidole</i> sp. | 1 | 0 | NA | NA |
| <i>Tetramorium</i> sp. | 3 | 0 | NA | NA |
| Total | 78 | 0.42 | 0.69 | 0.41 |

Aggression is the proportion of encounters in which invaders were attacked. Drag and Drop are proportions of aggressive encounters in which *M. sofina* dragged invaders to a cliff or cliff jumped with them

of 0.714 (Vogt and Appel 1999). Colony O₂ demand and CO₂ production were calculated by multiplying average colony size by average worker rates. Our estimates conservatively underestimate metabolic demands because ant metabolic rates may increase up to sevenfold with temperature and activity (Duncan and Crewe 1993) and we ignore metabolism of the queen, brood and young reproductives.

Nest defense

We examined the nest defense hypothesis by introducing foreign ants to *M. sofina* nests. We performed 80 introductions with eight species, including conspecifics from other colonies (Table 1). All species occurred near the nests, including two ant predators (*Cerapachys* sp., nocturnal *Camponotus* sp.), and are likely encountered in nature. We filmed 23 of the introductions. For each trial, we placed one foreign ant on or near an entrance and observed whether they could navigate the funnel, whether native workers detected the foreign ant on the funnel, and the nature of any aggressive responses.

Data analysis

All statistics were performed in R (R Core Team 2013). Regressions were reduced major axis regressions using the “lmodel2” package (Legendre 2011) to account for measurement error of independent variables (McArdle 1988). Variables were checked for normality with the Shapiro–Wilk test. Normal variables are presented as means with standard deviations, and non-normal ones as medians with interquartile ranges (IQR). Funnel length, entrance area and area ratio were log-transformed for regressions to meet normality assumptions. Interior area deviated from normality even with transformation, so we used untransformed values. Regressions of entrance characters on depth were

corrected for experimentwise error with the Holm–Bonferroni correction (Holm 1979).

Results

Nests

All 25 nests were on vertical surfaces, from 10 cm to 3 m above the ground. Nest chambers averaged 7.50 (\pm 2.8, $n = 14$) cm deep (Fig. 4). Funnels projected a median of 2 (IQR 1.25, $n = 22$) cm beyond the nest wall, with entrance and interior areas of 8.25 (IQR 6.68, $n = 25$) and 1.18 (IQR 1.18, $n = 23$) cm². Major and minor axes of entrances measured 4 (IQR 1.5) by 3 (IQR 1.5) cm ($n = 25$), and interiors 1.5 (IQR 0.5) by 1 (IQR 0.5) cm ($n = 23$). Funnel area ratios varied 14-fold, ranging from very flared (ratio 24) to nearly straight (ratio 1.7), with a median of 6.25 (IQR 6.31, $n = 23$). Neither funnel length ($r^2 = 0.006$, $P = 0.39$, $n = 14$) nor entrance area ($r^2 = 0.0002$, $P = 0.49$, $n = 14$) varied with nest depth. Funnels trended toward larger interiors ($r^2 = 0.18$, $P = 0.11$, $n = 14$) and were less flared in deeper nests ($r^2 = 0.25$, $P = 0.03$, $n = 14$). After correcting for experimentwise error, however, these effects are not significant (interior area $P = 0.33$, ratio $P = 0.12$). If real, it is likely because increased worker traffic in larger colonies requires larger interiors, reducing area ratios. Despite different substrates and mode of construction (alcoves versus excavated), rock and clay nests did not differ in nest depth (Kruskal–Wallis, $P = 0.35$, $n = 9$ vs. 5), funnel length (Kruskal–Wallis, $P = 0.81$, $n = 17$ vs. 5) or entrance area (Kruskal–Wallis, $P = 0.75$, $n = 19$ vs. 6). Of the four colonies where we removed entrance funnels, two had started rebuilding them the next day. We observed a fifth colony repairing a naturally damaged funnel using soil brought from within the nest. Because funnels did not vary with substrate, were sometimes constructed from soil carried up from the ground below, and were rebuilt after destruction, they are not artifacts of nest construction and likely serve an adaptive function.

Colonies and queens

Colonies were small but variable, ranging from 16 to 127 workers with an average of 62.5 (\pm 34, $n = 15$). While counting we placed workers in plastic trays coated with fluon. Unlike most ants, *M. sofina* workers gripped and clung to the coated tray, even when tilted sideways. This enhanced tarsal grip is reminiscent of that seen in arboreal ants and may be an adaptation to cliff dwelling (Federle et al. 2000, 2004).

Each colony contained an ergatoid (permanently wingless) queen (reviewed in Peeters 2012). Since queens cannot

fly, dispersal occurs on foot. Mating likely occurs at the nest, with foreign males flying to find virgin queens. Colony founding is dependent (Cronin et al. 2013)—before or after mating, a young queen walks to a new site with a group of nestmate workers. Dependent colony foundation would allow rapid construction of funnel entrances because colonies begin with a sizeable worker force, as opposed to species where new colonies are initiated by solitary queens.

Polydomy

We located three potentially polydomous colonies—one pair of nests 28 cm apart in rock, another pair 3 cm apart on a boulder (Fig. 2c), and three nests 25 and 13.5 cm apart in a clay bank (Fig. 2d). In the pair of rock nests, we transplanted two workers from one entrance to the other. In both cases, the worker ran inside as if it were her own nest. Among the three clay nests, we transplanted four workers. In two cases, the worker walked out of the entrance. The third ant groomed itself in the entrance, walked on the funnel, was antennated by a native worker without aggression and eventually walked away. In the fourth case, the introduced worker encountered a returning forager who ignored her, and then she entered as if it were her own nest. We twice observed workers walk from one clay nest and enter another without aggression—first a lone worker and then a group of several. We excavated the two rock nests and one of the clay nests and found no connecting tunnels. These observations, and the extreme proximity of the two boulder nests, suggest that *M. sofina* is facultatively polydomous.

Water exclusion

We pipetted water onto rock and clay nests, placing it on the substrate above the nest, the funnel neck, and upper and lower parts of the entrance. Water ran around the funnel or, when added directly to the entrance, ran to the lower lip and dripped off. Iodine solution did not diffuse through the funnel wall in any of the four permeability tests, remaining either inside or outside the funnel. Both assumptions of the water exclusion hypothesis—water diversion and impermeability—are thus supported. It is worth noting, however, that the same results would obtain with a simple tube rather than a funnel (Longino 2005).

Gas exchange

Workers averaged 1.028 (\pm 0.20) mg dry weight. Each would consume 1.25 μ l O₂ per h and produce 0.895 μ l CO₂ per h. A colony (average 62.5 workers) would consume 78.2 μ l O₂ per h and produce 56.0 μ l CO₂ per h, more than enough to raise CO₂ concentrations in a single chamber nest to over 12 times atmospheric levels (Cox and Blanchard

2000), especially in wet non-porous sandstone or clay. Even ignoring elevated respiration due to activity, hypoxia and hypercapnia are thus real dangers, supporting the assumption that diffusion is insufficient to meet metabolic demands.

The median area of gas exchange—the funnel entrance—was 6.25 times larger than the interior. By using funnels rather than simple tubes, colonies thus enhance diffusive gas exchange rates over sixfold. Moreover, if the funnels induce an internal air flow, then currents in the funnel interior should be over six times faster than in the entrance. By projecting the funnel 2 cm beyond the nest and flaring the entrance, colonies likely achieve major increases in nest air flow. Funnel dimensions are therefore consistent with a gas exchange function. At the same time, funnels did not vary with nest depth, which might be expected under the gas exchange hypothesis if depth is correlated with colony size and metabolic demands.

Defense

We performed 80 worker introductions of conspecifics and 7 co-occurring species to ten *M. sofina* nests. In two trials, the invader disappeared in the nest and was unobservable, so we discarded those data. All species successfully navigated the funnel, passing from funnel to substrate and vice versa. In addition, the funnels' large interior cross-sections allowed all species, even *Bothroponera* sp. several times the size of *M. sofina*, to enter the nest. Moreover, the presence of invaders on the funnel did not arouse native workers. Workers responded to invaders only when encountered directly. Similarly, workers did not respond to tapping or brushing of the funnel with forceps. The funnel thus functioned neither as an obstacle nor an alarm system.

In most cases (45 of 78), *M. sofina* responded timidly to invasions, showing no aggression and retreating into the nest (Table 1). In several cases, invading ants walked deep into the nest and remained there unmolested by workers, who retreated to other parts of the nest cavity. Workers responded aggressively to 33 introductions (42 %). In these cases, individual workers attacked invaders wherever they encountered them. Workers did not swarm to aid nest mates in combat, nor did they actively defend the nest entrance itself as Meliponine bees do (Roubik 2006). The funnel thus did not function as a defensive structure.

Four species, including conspecifics, were not attacked by *M. sofina* (Table 1). Workers ignored invaders or retreated on contact. Of four species that were sometimes attacked, two are ant predators (*Cerapachys* and nocturnal *Camponotus*) and likely more of a threat. When defending, *M. sofina* grasped an invader with its mandibles and tried to sting it. Combat was one-on-one and other workers rarely helped, even if fighting occurred in the nest. The defending

worker would drag the invader to the cliff, even if contact occurred deep in the nest. We checked for dragging behavior in 29 of 33 aggressive responses, and of these, 20 invaders (69 %) were dragged to the cliff. Once there, *M. sofina* would often drop off the cliff and fall up to a few meters onto the ground below, taking the invader with it (Supplemental Video). The ants separated upon hitting the ground, the *M. sofina* worker leaving the invader and climbing the cliff to return to its nest. This is reminiscent of directed aerial descent in arboreal ants, in which workers fall to escape predators and navigate back to their nest (Yanoviak et al. 2011). We are unaware, however, of other species that cling to enemy ants while doing so, and call the behavior cliff jumping. Of 29 aggressive responses checked for cliff jumping, 12 invaders (41 %) were dropped in this way. In one of these cases, *M. sofina* dropped the invader off the cliff without falling with it. Four trials with diurnal *Camponotus* occurred before we noticed these behaviors and were not scored. Though we recorded aggressive responses separately for each species, sample sizes are too small to tell if they differ in their treatment.

Discussion

The cliff dwelling lifestyle of *M. sofina* involves conspicuous architecture and striking defense behaviors. Colonies live in single chamber nests on sandstone cliffs, boulders and clay banks, and may occupy several closely spaced nests. All nests have projecting funnel-shaped entrances. Each colony has an ergatoid (permanently wingless) queen and reproduces by fission, allowing rapid construction of nests and funnel entrances. Funnels divert water and may ventilate the nest by increasing gas exchange and air flow rates, though we lack direct air flow measurements. Funnels serve no defense function, either as obstacles, alarm systems or actively defended structures. Workers are timid and rely on inaccessible nest locations rather than aggression for defense. When workers do defend the nest, they do so individually in one-on-one combat. Defenders often drag invaders onto exposed cliff faces and drop off while clinging to them, before climbing back up to their nest. *M. sofina* exhibits novel behaviors, provides a system for studying air flow and nest architecture, and illustrates the urgency of exploration in biodiversity hotspots.

Air flow dynamics are important to life at ant scales (Vogel 1994) and may drive the evolution of nest architecture (Cox and Blanchard 2000; Kleineidam and Rocas 2000; Kleineidam et al. 2001), but often go unrecognized. *M. sofina* and other funnel-building ants nest in wet impermeable substrates on vertical surfaces, where gas exchange by diffusion or vertical convection is unlikely to meet the metabolic or thermal demands of the colony or its

symbionts. The gas exchange hypothesis thus explains the recurrent evolution of funnel entrances across ant lineages as a response to similar nesting environments. A proposed ventilation system, however, may have other functions besides metabolism. Funnel-mediated air currents may regulate humidity or temperature, or disperse colony odors (Vogel et al. 1973; Weir 1973; Longino 2005). The latter may be especially important to species with ergatoid queens in which colonies attract males by scent (Peeters 2012; Shik et al. 2013). By dispersing colony odors and queen pheromones beyond the boundary layer, as well as being a visual landmark (Longino 2005), funnel entrances likely make it easier for *M. sofina* males to find colonies with unmated queens. The ventilation system postulated by the gas exchange hypothesis may play any of these roles.

Like many Malagasy ants (Fisher 2003), *M. sofina* has a restricted range. Galoko is one of five known localities, all within a small region of northwest Madagascar (AntWeb 2014). While *M. sofina* likely occurs in nearby unexplored forests, the region suffers from high levels of deforestation (Callmänder et al. 2009) and few of its remaining fragments are protected. Within fragments, *M. sofina* is patchily distributed because of its restricted microhabitat, and possibly its low dispersal ability, with sizeable populations limited to large rocky outcrops. Restricted range, lack of protection, and vulnerable life history characters conspire to threaten *M. sofina* with extinction by habitat destruction.

Malagidris sofina is one of several species restricted to Galoko and nearby regions (Callmänder et al. 2008, 2009). Like the ecosystems of Madagascar in general (Myers et al. 2000; Ganzhorn et al. 2001; Goodman and Benstead 2005), the remaining forests around Galoko are threatened, largely unexplored and likely harbor undiscovered endemic species (Callmänder et al. 2008, 2009). The insights derived from *M. sofina* illustrate the urgency and scientific value of further exploration and protection of this area.

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