

RESEARCH ARTICLE

Water surface locomotion in tropical canopy ants

S. P. Yanoviak^{1,*} and D. N. Frederick²**ABSTRACT**

Upon falling onto the water surface, most terrestrial arthropods helplessly struggle and are quickly eaten by aquatic predators. Exceptions to this outcome mostly occur among riparian taxa that escape by walking or swimming at the water surface. Here we document sustained, directional, neustonic locomotion (i.e. surface swimming) in tropical arboreal ants. We dropped 35 species of ants into natural and artificial aquatic settings in Peru and Panama to assess their swimming ability. Ten species showed directed surface swimming at speeds >3 body lengths s^{-1} , with some swimming at absolute speeds >10 $cm s^{-1}$. Ten other species exhibited partial swimming ability characterized by relatively slow but directed movement. The remaining species showed no locomotory control at the surface. The phylogenetic distribution of swimming among ant genera indicates parallel evolution and a trend toward negative association with directed aerial descent behavior. Experiments with workers of *Odontomachus bauri* showed that they escape from the water by directing their swimming toward dark emergent objects (i.e. skototaxis). Analyses of high-speed video images indicate that *Pachycondyla* spp. and *O. bauri* use a modified alternating tripod gait when swimming; they generate thrust at the water surface via synchronized treading and rowing motions of the contralateral fore and mid legs, respectively, while the hind legs provide roll stability. These results expand the list of facultatively neustonic terrestrial taxa to include various species of tropical arboreal ants.

KEY WORDS: Aquatic, Behavior, Forest, Formicidae, Neustonic, Skototaxis

INTRODUCTION

Efficient locomotion at the air–water interface is relatively uncommon in nature (Vogel, 1994). Most terrestrial arthropods are helpless when they fall onto water, in part because their small body size makes them vulnerable to entrapment by surface tension forces. Additionally, the relatively low physical resistance of water to slender kicking appendages often leads to a futile struggle ending in death via drowning or predation. Conspicuous exceptions to these generalities include the specialized water-treading behaviors and morphologies of neustonic insects and spiders (Andersen, 1976; Milne and Milne, 1978; Vogel, 1994; Hu et al., 2003). For species lacking such traits, escape from the water surface usually is fortuitous.

The very specialized legs of obligate pelagic and neustonic taxa such as diving beetles and water striders facilitate efficient locomotion below or on the water surface (Nachtigall, 1974), but are relatively ineffective and clumsy on land. The gaits of these insects

often are kinematically distinct from the alternating tripod gait used by terrestrial species in the same clades (Andersen, 1976). By contrast, riparian arthropods frequently tread on both land and water with high efficiency using the same gaits and appendages. For example, the hydrophobic tarsi of riparian *Hydrophorus* flies allow them to alight on water or vegetation (Burrows, 2013), and the modified hind legs of tridactylid grasshoppers facilitate large jumps from both land and water (Burrows and Picker, 2010; Burrows and Sutton, 2012). Many spiders also locomote equally well on water and land (Stratton et al., 2004); some use a modified gait when on water while others do not (Suter and Wildman, 1999; Suter et al., 2003; Suter, 2013). Although less common, a few entirely terrestrial insect taxa (e.g. mantids, cockroaches) are also capable of traversing a water surface with modified or unmodified gaits, depending on the species (Franklin et al., 1977; DuBois and Jander, 1985).

As small, terrestrial and obligately cursorial organisms, ants seem particularly unlikely to interact favorably with water. Workers of some species use water surface tension to their advantage when foraging (Young and Hermann, 1980; Dejean and Suzzoni, 1997), but complete immersion typically is problematic for ants. Nonetheless, a few ant species are able to locomote on or in water remarkably well. In the simplest case, entire colonies form rafts of workers and brood on the water surface. This behavior was described in detail for *Solenopsis* (Adams et al., 2011; Mlot et al., 2011), but also occurs in some *Wasmannia* and *Pheidole* species (Robson, 2010; S.P.Y., personal observation). Other rainforest taxa, such as *Ectatomma ruidum* in Central America, will voluntarily walk beneath the surface of puddles on the forest floor (S.P.Y., personal observation), and workers of *Camponotus schmitzi* forage for insect prey by crawling or swimming into the water held by *Nepenthes* pitchers in Asia (Bohn et al., 2012). Directed locomotion on water surfaces is known in only a few ant taxa, including *Polyrhachis sokolova* workers of Australian mangrove forest (Robson, 2010), *Camponotus* spp. in Malaysia and North America (DuBois and Jander, 1985), and certain leaf cutter ants (*Acromyrmex lundii carli*) inhabiting Amazonian flooded forest (Adis, 1982). Here we describe the occurrence, basic kinematics and directionality of water surface locomotion in various Neotropical ants.

Ants are among the most abundant and conspicuous arthropods in tropical forests, and many species nest and forage in tree crowns high above the ground (Hölldobler and Wilson, 1990; Rico-Gray and Oliveira, 2007; Klimes et al., 2012). Arboreal ants frequently fall from the canopy to the forest understory (Haemig, 1997; Longino and Colwell, 1997), where they face unfamiliar predators and complex terrain (Yanoviak et al., 2011). Tropical flooded forests and riparian areas are especially dangerous; they are often inhabited by fish that consume terrestrial insects trapped in the water surface (Saint-Paul et al., 2000; Small et al., 2013). Lost workers are costly to their colonies, and some species avoid landing in the hazardous understory by gliding to nearby tree trunks (Yanoviak et al., 2005). However, many species do not glide, and surveys in lowland forest of Panama show that ants constitute ca. 70% of wingless arthropods falling from the canopy to the understory (D.N.F. and S.P.Y.,

¹Department of Biology, University of Louisville, 139 Life Sciences Building, Louisville, KY 40292, USA. ²Department of Biology, University of Arkansas at Little Rock, Little Rock, AR 72204, USA.

*Author for correspondence (steve.yanoviak@louisville.edu)

unpublished). Given that falling ants will occasionally land in water, it is likely that some species possess traits facilitating their escape from a water surface.

Most foraging ants navigate using a combination of visual and chemical senses (Hölldobler, 1980; Hölldobler and Wilson, 1990; Nicholson et al., 1999), and gliding canopy ants use visual cues to locate tree trunks during a fall (Yanoviak and Dudley, 2006). Likewise, ants landing on water should use local cues to direct their escape maneuvers toward nearby emergent objects, as do swimming mantids (Miller, 1972). Other studies of ants treading on water suggest that they specifically move toward dark objects [i.e. skototaxis (DuBois and Jander, 1985)]. Various insects exhibit skototaxis, although reasons for the behavior are not always obvious (Taylor, 1988; Campan, 1997). Skototaxis may be especially effective in ecotonal, riparian and flooded forest settings; the water surface reflects ambient light, and tree trunks consequently are the darkest nearby landmarks (Campan, 1997). Indeed, Amazonian ground-dwelling beetles use skototaxis to locate tree trunks when traversing seasonal floodwaters (Irmler, 1973).

The principal objective of this study was to document surface swimming in tropical ants and the distribution of this behavior among common arboreal ant taxa. We tested four predictions. First, we expected that swimming is limited to relatively large-bodied species because of the strong surface tension forces experienced by small floating objects (DuBois and Jander, 1985; Vogel, 1994). Second, we predicted a negative relationship between swimming and aerial gliding behavior among ant taxa, as gliding ants presumably are less likely to fall into the forest understory (Yanoviak et al., 2005; Yanoviak et al., 2011). Third, we expected that ants use a modified gait to swim (DuBois and Jander, 1985), and that swimming kinematics are relatively consistent among taxa. Finally, we predicted that swimming ants escape from the water using skototaxis (i.e. they direct their surface locomotion toward dark emergent objects).

RESULTS

Over half (57%) of the 35 tested species exhibited some swimming ability, and half of those were considered strong swimmers (Table 1). Although the distinction between strong and weak

Table 1. Mean (\pm s.e.m.) mass and swimming speed of ant species tested for surface swimming behavior in Peru and/or Panama

Taxon	N	Mass (mg)	Speed (cm s ⁻¹)	Group
Dolichoderinae				
<i>Azteca trigona</i> Emery	5	4.5 \pm 1.95	3.2 \pm 1.86	Strong
<i>Dolichoderus bispinosus</i> (Olivier)	5	5.3 \pm 0.50	0.7 \pm 0.21	Weak
Ecitoninae				
<i>Eciton hamatum</i> (Fabricius)	10	15 \pm 10.2	2.4 \pm 0.26	Weak
Ectatomminae				
<i>Ectatomma ruidum</i> (Roger)*	8	8.9 \pm 1.82	0.9 \pm 0.21	Weak
<i>E. tuberculatum</i> (Olivier)	7	22 \pm 2.9	1.4 \pm 0.47	Weak
<i>Gnamptogenys concinna</i> (Smith)	1	48.3	1.56	Weak
<i>G. regularis</i> (Santschi)	7	<1	0	None
Formicinae				
<i>Camponotus senex</i> Smith	5	8.3 \pm 0.95	2.5 \pm 0.81	Strong
<i>C. sericeiventris</i> (Guérin-Méneville)	5	62 \pm 22.4	2.7 \pm 0.62	Strong
<i>Gigantiops destructor</i> (Fabricius)	9	18 \pm 1.7	10.9 \pm 0.96	Strong
Myrmicinae				
<i>Atta cephalotes</i> (Linnaeus)	5	31 \pm 5.3	0	None
<i>Acromyrmex volcanus</i> Wheeler	6	28 \pm 9.2	0	None
<i>Cephalotes atratus</i> (Linnaeus)	51	25 \pm 0.1	0	None
<i>C. basalis</i> (Smith)	5	7.5 \pm 2.28	0	None
<i>C. christophersenii</i> (Forel)	5	2.9 \pm 0.11	0	None
<i>C. umbraculatus</i> (Fabricius)	3	5.7 \pm 3.00	0	None
<i>Crematogaster carinata</i> Mayr	4	0.9 \pm 0.16	0	None
<i>Daceton armigerum</i> (Latreille)	10	26 \pm 1.9	<1	Weak
<i>Nesomyrmex anduzei</i> (Weber)	1	2.8	0	None
<i>Pheidole</i> sp. 1	10	<1	0	None
<i>Pheidole</i> sp. 2*	3	<1	0	None
<i>Procryptocerus belti</i> Forel	9	1.4 \pm 2.00	0	None
<i>Solenopsis</i> sp. 1	5	<1	0	None
<i>Solenopsis</i> sp. 2*	2	<1	0	None
<i>Wasmannia rochai</i> Forel	7	<1	0	None
Paraponerinae				
<i>Paraponera clavata</i>	6	162 \pm 18.5	<1	Weak
Ponerinae				
<i>Hypoponera distinguenda</i> (Emery)	10	6.4 \pm 0.37	4.6 \pm 0.75	Strong
<i>Odontomachus bauri</i> Emery	5	17 \pm 1.8	10.2 \pm 1.09	Strong
<i>O. nr. ruginodis</i>	4	6.9 \pm 0.37	5.3 \pm 0.68	Strong
<i>Pachycondyla apicalis</i> (Smith)*	7	28 \pm 1.4	6.0 \pm 2.11	Strong
<i>P. foetida</i> (Linnaeus)	5	28 \pm 1.9	8.6 \pm 0.77	Strong
<i>P. nr. harpax</i>	5	6.1 \pm 0.40	1.2 \pm 0.36	Weak
<i>P. villosa</i> (Fabricius)	5	51 \pm 4.1	8.4 \pm 1.14	Strong
Pseudomyrmecinae				
<i>Pseudomyrmex gracilis</i> (Fabricius)	1	10.8	<1	Weak
<i>P. oculatus</i> (Smith)	6	1.1 \pm 0.07	0.8 \pm 0.41	Weak

Each tested species was assigned to one of three groups based on a semi-quantitative assessment of swimming ability as described in the Materials and methods. *Epigeic species.

categories (see Materials and methods) was based on relative swimming speed, mean (\pm s.e.m.) absolute speed also was significantly higher for ants in the strong ($6.0 \pm 0.74 \text{ cm s}^{-1}$) versus weak ($1.1 \pm 0.70 \text{ cm s}^{-1}$) group (Wilcoxon $Z=3.64$, $P=0.0003$). The fastest swimmers were *Gigantiops destructor* and *Odontomachus bauri* (Table 1), with some individuals exceeding 16 cm s^{-1} . Assignment of ants to the strong category was unambiguous; workers of these species made consistent, rapid and directed forward progress across the water. Likewise, all ants in the none category clearly were helpless at the water surface. This outcome is partially attributed to body size, as ants in the none group were significantly smaller (mean mass \pm s.e.m. = $7.2 \pm 7.49 \text{ mg}$) than ants in the weak ($30.6 \pm 9.17 \text{ mg}$) and strong ($22.5 \pm 9.67 \text{ mg}$) groups (Kruskal–Wallis $\chi^2=9.38$, d.f.=2, $P=0.009$).

Various species of ants in the weak category were capable of directed paddling locomotion across the water surface, but their progress was inconsistent. Some weak swimmers such as *Pseudomyrmex* spp. and *Gnamptogenys concinna* clearly tread across the water surface in a directed manner, but were unable to climb the meniscus at the edge of the pan, suggesting that they would not be able to escape if directed to an emergent object. *Daceton armigerum* workers typically were helpless in the water for 30–60 s before swimming forward at low speed (generally $<1.0 \text{ cm s}^{-1}$). Despite their slow progress, *D. armigerum* workers have good vision and frequently directed their struggling effort toward any emergent or floating objects within 10–15 cm of their location. By contrast, swimming *Pachycondyla villosa* commonly avoided or traversed floating debris before continuing toward the shore or to an emergent stem.

Phylogenetic analysis revealed a strong phylogenetic signal in the swimming performance data ($K=1.24$), and the distribution of strong swimming suggests multiple independent origins (i.e. parallel evolution) of the behavior among formicine, dolichoderine and ponerimorph clades (Fig. 1). Although there was a negative relationship between swimming and gliding performance ($r=-0.15$), the pattern was not statistically significant (GLS log-likelihood = -4.46 , $P=0.65$). Nonetheless, strong swimming behavior and gliding behavior tended to be negatively associated among ant genera, co-occurring only within *Camponotus* (Fig. 1).

Pachycondyla villosa workers dropped onto the surface of a fishless pond in Panama successfully evaded more agile neustonic predators (mainly gerrids; supplementary material Movie 1). By contrast, five haphazardly collected *Atta cephalotes* workers tested in the same manner were immediately attacked and eventually killed by gerrids. Many ants dropped from the Amazon Conservatory for Tropical Studies (ACTS) bridge were attacked by fish and carried beneath the water surface within a few seconds of landing. Often the ants were not seen again; however, fish commonly rejected *P. villosa* and *Cephalotes atratus* after an initial attack. The rejected ants emerged at the surface and either continued struggling (*C. atratus*) or continued swimming toward an emergent object (*P. villosa*). In a few cases, fish were observed to hold an ant partially exposed in the premaxillary region of the mouth (i.e. between their ‘lips’) for up to 15 s before ingestion or rejection, presumably to flush the ant’s chemical defenses or to determine prey quality (Eisner and Aneshansley, 2000). Unfortunately, logistical constraints prevented us from collecting and identifying the fish observed in this study.

Kinematics

Swimming kinematics were qualitatively very similar among the three recorded species; each used a modified alternating tripod gait

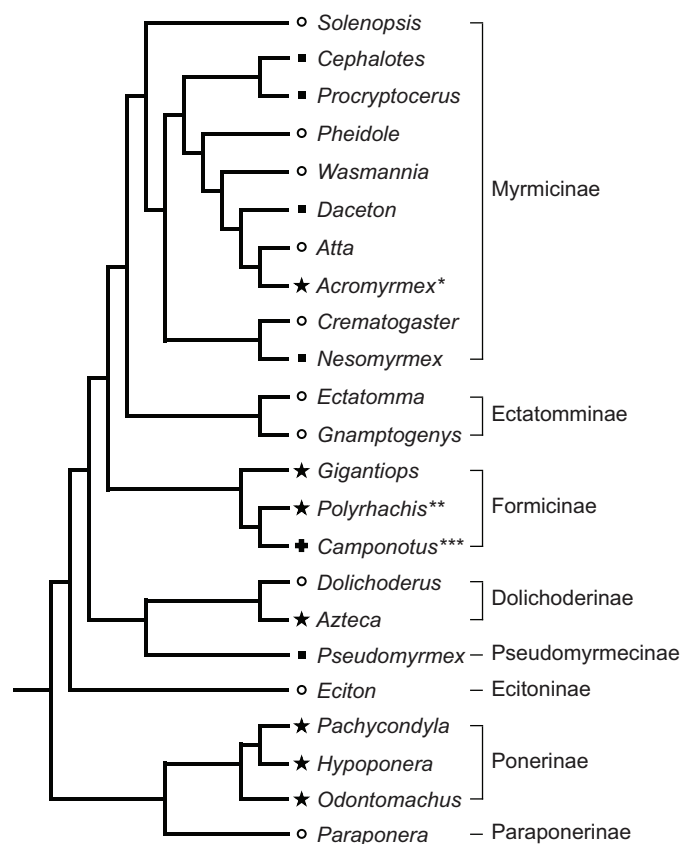


Fig. 1. The distribution of strong swimming and gliding behavior among ant genera. Star, swimming; filled square, gliding; plus sign, both swimming and gliding; open circle, neither swimming nor gliding. The tree was redrawn from Moreau and Bell (Moreau and Bell, 2013); branch lengths have no meaning. Taxa shown include only those experimentally tested for both behaviors in this study, or in combination with results of other studies; *from Adis (Adis, 1982), **from Nielsen (Nielsen, 1997), ***also see DuBois and Jander (DuBois and Jander, 1985) and Bohn et al. (Bohn et al., 2012).

to locomote on the water surface (Figs 2–4, supplementary material Movie 2). Video analysis showed that the majority of the thrust force is generated by synchronized movement of the contralateral fore and mid legs through a ca. 90 deg arc (Table 2), while the hind leg ipsilateral to the thrusting foreleg functions primarily as a stabilizer. The forelegs generated thrust via anterior-to-posterior movement with a relatively small lateral displacement, whereas the mid legs generated thrust via posterolateral rowing motions (i.e. with a large horizontal component; Figs 2–4, supplementary material Movie 2). Both hind tarsi simultaneously contact the water for ca. 20 ms during each stroke cycle in *Pachycondyla* spp. (Figs 2, 3) and for most of the stroke cycle in *O. bauri* (Fig. 4, supplementary material Movie 2); one hind leg (ipsilateral to the thrusting foreleg) enters the water while the other is withdrawn. All three species swim with the ventral surface of the mesosoma in constant contact with the water and the bulk of the ant body remaining well above the surface. The apices of the gaster and mandibles occasionally touch the water in *Pachycondyla* spp., but rest continuously on the water surface in swimming *O. bauri*. Unlike *Camponotus* spp., which swim by completely immersing at least one pair of legs (DuBois and Jander, 1985; Bohn et al., 2012), only the tarsus of each leg consistently penetrated the water surface in the ants we observed. Also, each leg was completely withdrawn from the water and moved anteriorly to initiate the subsequent stroke.

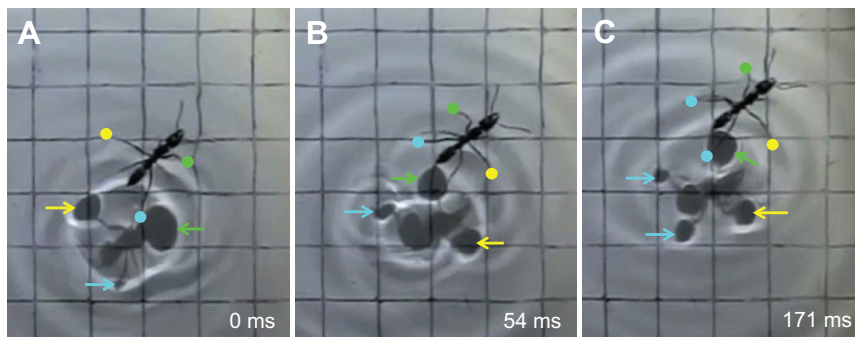


Fig. 2. Leg positions of a *Pachycondyla foetida* worker during locomotion at the water surface. Images are still frames from a high-speed video (240 frames s^{-1}). Colored circles indicate approximate contact points of forelegs (green) mid legs (yellow) and hind legs (blue). Arrows indicate the corresponding meniscus shadow for each contact point. The time between A and B is approximately half of a full stroke cycle for this ant. The background grid is 1×1 cm.

Differences in the average stroke amplitude (maximum angle traversed by a leg) among leg pairs nested within the three focal species (Table 2) provide quantitative verification of the minimal role of the hind legs in generating propulsive force. Specifically, stroke amplitude was significantly smaller for the hind legs than the fore and mid legs, which did not differ from each other (nested ANOVA: species, $F_{2,36}=0.82$, $P=0.44$; legs within species, $F_{6,36}=41.0$, $P<0.0001$; Table 2). Subsequent Tukey's honest significant difference tests (using data for each leg pair separately) showed that stroke amplitude for the mid and hind legs differed marginally among species (Table 2). The duration of a complete stroke cycle ranged from 129 to 204 ms for *P. villosa*, from 146 to 217 ms for *P. foetida* and from 158 to 275 ms for *O. bauri*. Stroke frequency (measured as the number of complete stroke cycles of the mid legs per second) was lower for *O. bauri* than for either *Pachycondyla* species, which did not differ from each other (ANOVA: $F_{2,12}=4.24$, $P=0.04$; Table 2).

Directed swimming

Most (96%) of the *O. bauri* workers dropped into the Barro Colorado Island (BCI) pool began swimming to the edge within 5 s of landing on the water surface. The remaining individuals (4%) either did not swim or swam haphazardly for several minutes without reaching the edge of the pool. Swimming *O. bauri* workers showed very clear directed locomotion toward the black pole, successfully reaching the target and escaping from the water in 87% of trials (supplementary material Movie 3). Consequently, the distribution of *O. bauri* swimming directions was significantly biased toward the black target regardless of its location ($r=0.811$, $P<0.0001$; Fig. 5). By contrast, the distribution of *O. bauri* swimming azimuths did not differ from random when the white target was present ($r=0.151$, $P=0.12$); the ants had difficulty locating the white target, even when passing <5 cm from it. Nonetheless, ants emerged from the pool on the white pole in ca. 23% of trials. All such escapes occurred when the target was located in the north or east position in the pool. Subsequent examination of the surrounding area suggested that, in the absence of a nearby black target, the ants oriented toward a dark wall located a few meters to the east of the pool.

Pachycondyla villosa workers dropped from the bridge at ACTS showed no directional bias ($r=0.046$, $P=0.98$), but *Gigantiops destructor* swam westward with higher frequency than any other direction ($r=0.738$, $P=0.001$). Trials for *G. destructor* were always run in the afternoon (ca. 16:00 h), thus we cannot determine whether they used solar cues when swimming, or swam toward a landmark that escaped our attention.

DISCUSSION

Yanoviak et al. (Yanoviak et al., 2005) posited that aerial gliding behavior in arboreal ants has evolutionary origins in flooded forests, where death by predation (or drowning) provides significant selection pressure. Here, we show that many species of Neotropical arboreal ants potentially avoid predation or drowning by swimming across the surface of water following a fall. Prior descriptions of swimming behavior in ants either focused on specialized cases driven by specific habitat associations (Adis, 1982; Nielsen, 1997; Bohn et al., 2012) or lacked a broader context (DuBois and Jander, 1985). Our observation that swimming behavior occurs in multiple ant genera distributed among different clades suggests parallel evolution in response to strong selection pressure. Although not statistically significant, the trend for a negative phylogenetic association between swimming and gliding behaviors suggests that an evolutionarily successful arboreal lifestyle requires mechanisms to either avoid or survive the hazards of falling.

Our goal was to examine the distribution of swimming across a large number of ant genera to provide a framework for preliminary phylogenetic analyses. However, we observed considerable variation in swimming performance among species within genera (e.g. *Pachycondyla* spp.). Similarly, Adis (Adis, 1982) reported that *Acromyrmex lundii* workers walk or swim across the water surface when foraging in flooded Amazonian forest, but the *A. volcanus* workers we collected from tree crowns in Panama could not swim. Thus, data from many more species and genera are needed to fully resolve the evolutionary patterns underlying the behavior. This study also was limited to Neotropical species, and broadening the survey to include arboreal and epigeic species in Paleotropical and other regions would be informative.

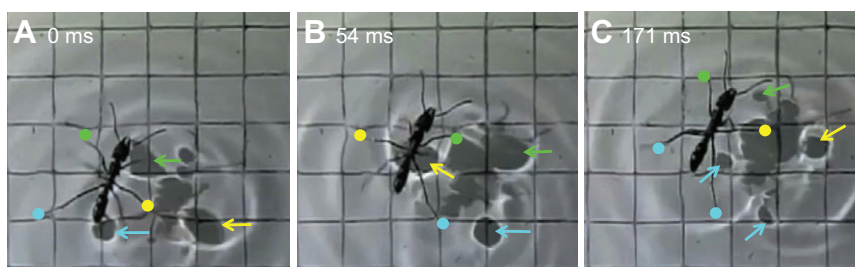


Fig. 3. Leg positions of a *Pachycondyla villosa* worker during locomotion at the water surface. See Fig. 2 legend for details.

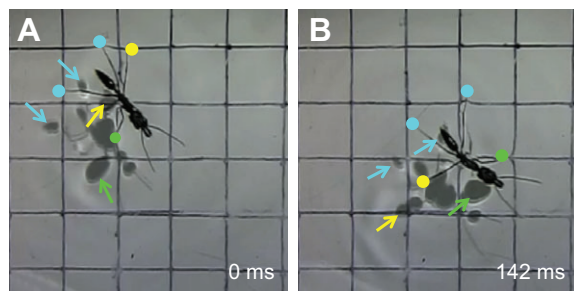


Fig. 4. Leg positions of an *Odontomachus bauri* worker during locomotion at the water surface. See Fig. 2 legend for details.

The main forces that govern aquatic locomotion are drag and buoyancy, whereas those that govern terrestrial locomotion are gravity and inertia (Vogel, 1994). Few animals are equipped to face both challenges, and interactions between body size and water surface tension greatly limit the size of organisms that can effectively tread at the air–water interface (Vogel, 1994). Results of the present study indicate that constraints on locomotion imposed by surface tension are stronger for ants at the low end of the body size distribution, as predicted. Additional studies (e.g. focusing on continuously polymorphic species) are needed to clarify the relevance of body size to swimming performance in ants.

For simplicity, we treated any directed locomotion at the water surface as ‘swimming’ and did not distinguish among different types of swimming postures (i.e. surface treading versus leg immersion). However, our observations and the results of other studies indicate that there is considerable interspecific variation in the amount of leg and body immersion associated with this behavior. The fastest swimming ants observed in this study generally maintained the bulk of their body at or above the water surface, with the swimming legs partially and intermittently immersed. This contrasts with the much deeper leg and body immersion reported for swimming *Camponotus* spp. (DuBois and Jander, 1985; Bohn et al., 2012) and *Polyrhachis sokolova* (Robson, 2010). The latter will also tread on the water surface (BBC, 2005). Thus, swimming posture can also vary intraspecifically, presumably in a context-dependent manner.

Our field observations and laboratory-based recordings suggest that *Pachycondyla* spp. and *O. bauri* employ a drag-based swimming mechanism, i.e. their legs provide propulsion similar to boat oars and the tarsi of galloping water spiders (Suter et al., 1997; Suter and Wildman, 1999). However, this assessment is preliminary because quantification of the relative contributions of drag, bow wave, surface tension and other forces was beyond the scope of this project. Likewise, we did not measure the differential wettability of ant body parts, which is another potentially important variable in

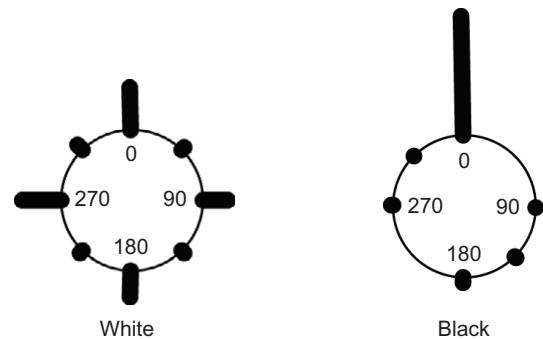


Fig. 5. The distribution of *Odontomachus bauri* swimming direction relative to black and white targets in an experimental pool. Stacked points on the perimeter of each circle represent the proportion of ants that swam in a given direction (estimated to the nearest 45 deg) relative to the position of the target, which was normalized as 0 deg in each trial for analysis. Numbers in the circles are degrees. $N=82$ trials with the black target present and $N=96$ trials with the white target present.

their interaction with the water surface (Suter, 2013). Detailed force and hydrophobicity analyses have been conducted for other taxa (Hu and Bush, 2010; Suter, 2013) and provide good models for future studies of water surface locomotion in ants.

The kinematic features of swimming in terrestrial arthropods are highly variable among taxa (Miller, 1972; Andersen, 1976; Franklin et al., 1977). Similar inconsistencies occur among ants. The basic swimming kinematics we observed in *Pachycondyla* spp. and *O. bauri* are very different from those described for *Camponotus americanus* (DuBois and Jander, 1985), and only superficially similar to those of *C. schmitzi* (Bohn et al., 2012). All of these species use their forelegs for thrust generation (kinematically approximating the treading motion used on land), but *C. americanus* uses its mid legs as a rudder, not for propulsion. Our focal species and *C. schmitzi* are comparable with respect to the use of a modified alternating tripod gait for swimming. However, given that all legs of *C. schmitzi* are completely immersed, the hind legs presumably function relatively less as roll stabilizers. Finally, the duration of each complete stroke cycle in swimming *C. americanus* [760 ms (DuBois and Jander, 1985)] was much longer than for *C. schmitzi* [ca. 107 ms (Bohn et al., 2012)] and for our focal species (maximum of 275 ms). Collectively, these differences support the conclusion that swimming, like gliding (Yanoviak et al., 2005), is effected by different morphological and kinematic mechanisms in different taxa. Thus, appropriate extensions of this work could include analyses of synchronized, multiaxial recordings of various ant taxa to provide a comprehensive assessment of ant swimming kinematics and their phylogenetic basis.

Table 2. Mean (\pm s.e.m.) mass, stroke frequency (number of complete stroke cycles per second) and per-leg stroke amplitude in swimming workers of *Odontomachus bauri*, *Pachycondyla foetida* and *P. villosa*

	<i>Odontomachus bauri</i>	<i>Pachycondyla foetida</i>	<i>P. villosa</i>
Mass (mg)	16.0 \pm 0.35 ^a	27.9 \pm 1.86 ^b	50.8 \pm 1.88 ^c
Stroke frequency (Hz)	4.8 \pm 0.58 ^a	5.8 \pm 0.28 ^b	6.4 \pm 0.37 ^b
Stroke amplitude (deg)			
Forelegs	90 \pm 6.6 ^a	88 \pm 3.4 ^a	93 \pm 10.0 ^a
Mid legs	90 \pm 7.5 ^a	70 \pm 1.0 ^b	76 \pm 4.8 ^{a,b}
Hind legs	27 \pm 3.0 ^{a,b}	34 \pm 1.2 ^a	23 \pm 2.0 ^a

Stroke amplitude was measured as the average arc (deg) traveled by each leg in a leg pair in three to seven complete cycles per ant. Thus, results reported here are the means of the per-ant averages for $N=5$ ants of each species. Within a row, similar letters indicate means that do not differ based on *post hoc* Tukey's honest significant difference tests. Stroke frequency $N=15$ for each species.

Many ant species that swim well also have relatively large eyes and presumably have good vision. The visual acuity of most ants remains unstudied, but some species use visual canopy maps to navigate through complex rain forest (Hölldobler, 1980; Baader, 1996), and others use celestial cues for orientation when local landmarks are scarce (Wehner, 1997). Swimming workers of *O. bauri* exhibited strong skototaxis, as also shown for Amazonian beetles (Irmler, 1973) and suggested for swimming *C. americanus* ants (DuBois and Jander, 1985). Skototaxis is considered a fundamental step in the evolution of more complex orientation behaviors, especially for organisms that depend on terrestrial landmarks (Campan, 1997), such as forest-dwelling ants (Hölldobler, 1980). For arboreal ants, skototaxis and its derivatives [e.g. perigrammotaxis (orientation to contrasting edges)] appear to facilitate finding tree trunks in a variety of circumstances, including gliding (Yanoviak and Dudley, 2006; Yanoviak et al., 2011). Here we show that swimming *O. bauri* workers visually target emergent landmarks, similar to swimming mantids (Miller, 1972). However, we cannot exclude the possibility that swimming ants use mechanical cues [e.g. rebounding surface waves (Bendele, 1986)] alone or in combination with vision to locate the shore or emergent objects. Observations of swimming behavior in ants with experimentally occluded vision (Miller, 1972) would clarify the importance of such alternatives.

In summary, wingless arthropods (especially ants) frequently fall from tree crowns and land in the understory (Haemig, 1997; Longino and Colwell, 1997; D.N.F. and S.P.Y., unpublished data). This 'arthropod rain' phenomenon is an important source of nutrient export from the forest canopy to the understory (Mason and MacDonald, 1982; Pringle and Fox-Dobbs, 2008), and is a key mechanism in the ecological coupling of terrestrial and aquatic habitats (e.g. Nakano et al., 1999; Small et al., 2013). Here we show that many species of tropical arboreal ants potentially evade predators and avoid drowning by treading in a rapid and directed manner across the water surface toward emergent objects or the shoreline. These results suggest at least three avenues for further research. First, a similar survey of swimming in Palearctic species would strengthen our understanding of the evolution of the behavior. In particular, we predict that *Oecophylla* spp. are strong swimmers because of their large size and good vision, whereas *Cataulacus* spp. are non-swimmers because of their behavioral and morphological convergence with *Cephalotes* spp. (Yanoviak et al., 2008). Second, studies of swimming behavior conducted in experimental settings with and without predators (especially fish) would clarify the relative importance of different potential selective agents (e.g. drowning and predation) in the evolution of swimming. Our field observations in Peru and Panama showed that ants on the water surface are regularly rejected or avoided by predatory fish. Finally, more refined studies of swimming kinematics (e.g. Bohn et al., 2012) and orientation cues (e.g. Irmler, 1973; Campan, 1997) within and among ant species are needed as described above.

MATERIALS AND METHODS

Field work was conducted at two lowland forest sites during May through July 2010–2013. The first site (hereafter, ACTS) is lowland primary forest managed by the Amazon Conservatory for Tropical Studies, 65 km NE of Iquitos, Peru (03.25°S, 72.91°W). The second site (hereafter, BCI) includes the seasonally moist forest and laboratory facilities managed by the Smithsonian Tropical Research Institute on Barro Colorado Island, Panama (09.15°N, 79.85°W). Additional information about these sites is available elsewhere (Leigh et al., 1996; Vásquez Martínez, 1997; Madigosky and Vatnick, 2000).

Swimming trials

We tested four epigeic and 31 arboreal or semi-arboreal ant species for swimming behavior (Table 1). Ants used in swimming trials were collected with forceps from leaf litter and low vegetation, and by baiting tree trunks and branches with a mixture of canned tuna and honey. Tree crowns were accessed by climbing with the single rope technique (Perry, 1978). We tested up to 51 workers of each species, and groups of workers were collected from different colonies when possible. Ants were housed individually in plastic vials for <24 h before trials, and each ant was weighed to the nearest 0.1 mg on an electronic balance. Very small ants were weighed in groups of several workers to determine their average individual mass.

The test procedure at the ACTS field site consisted of dropping ants individually from a foot bridge above a natural area of standing water in flooded forest connected to a permanent stream channel. The bridge and associated water surface were shaded by the forest canopy. Individual ant workers were placed into a 4-dram plastic vial coated internally with Fluon® PTFE-30 (BioQuip Products, Inc., Gardena, CA, USA). The vial was inverted to release the ant into free fall ca. 5 m above the water. We noted the general behavior of each ant on the water surface, and we measured its swimming progress with a stopwatch and laser distance meter (Disto D5; Leica Geosystems, Inc., Norcross, GA, USA). We used floating debris as reference points to ensure the accuracy of distance measurements. Only rectilinear, sustained locomotion for >1 m was used in velocity calculations. The stopwatch was started when the ant landed on the water and the time intervals between major events (e.g. fish attack and escape) were noted.

Swimming trials at BCI were performed in a shallow vinyl pool (183 cm diameter × 40 cm depth) housed within a screened outdoor enclosure. The pool contained tap water to a depth of ca. 10 cm, and a 10×10 cm grid was drawn on the bottom to provide a reference scale for measurements of ant speed and direction. We dropped individual worker ants from a height of 1.5 m onto the water surface in the center of the pool using forceps or a Fluon-coated vial (see above). Up to 10 swimming trials were conducted per ant species; a different worker was used in each trial and all trials were conducted in a consistent manner under similar conditions. We noted the time of day, and air and water temperature at the start of each trial. We recorded a 30 s video of each ant's swimming behavior under windless conditions using a compact digital video camera recording at 30 frames s⁻¹ and mounted ca. 1.8 m above the pool. Workers of swimming species typically began unambiguous directed movement immediately after landing on the water.

We quantified ant swimming speed in the BCI pool using NIH ImageJ software following basic protocols established for swimming spiders (Suter et al., 1997; Suter et al., 2003). A 10 s frame set was cut from each video beginning when the ant moved in a directed manner across the surface of the water. We calibrated distances for each recording by measuring four of the pool grid lines with linear measurement tools in ImageJ. We then measured the incremental displacement of each ant during rectilinear swimming as the hypotenuse of the change in *X* and *Y* coordinates in multiple frames of the image stack. Average velocity was calculated as the slope of the regression of displacement values against time.

Ant species were assigned to one of three groups based on a semi-quantitative assessment of swimming ability. The 'strong' group included species that consistently exhibited directed locomotion across the water surface at rates ≥3 body lengths (BL) s⁻¹. The 'weak' group included species of ants capable of directed locomotion across the water at rates <3 BL s⁻¹. Finally, the 'none' group included species for which 50% or more of the workers showed no directed locomotion at the water surface (Table 1). Voucher specimens of all tested species were deposited at the Fairchild Museum in Panama and at the University of Louisville, KY, USA.

Kinematics

Following protocols established elsewhere (DuBois and Jander, 1985; Suter et al., 2003), we quantified swimming leg kinematics for *O. bauri* and two *Pachycondyla* species (*P. foetida* and *P. villosa*) by recording their movement across a water surface in the laboratory (supplementary material Movie 2). Five workers of each species were weighed and then individually video-recorded at 240 frames s⁻¹ (Casio EX-ZR200, Casio, Inc., Tokyo, Japan) as they tread across the water surface in a shallow, white, rectangular

pan (20×30 cm) with a 1 cm grid drawn on the bottom. The pan contained water to a depth of 2 cm, the camera was positioned ca. 15 cm above and orthogonal to the water surface, and the field of view was illuminated with an LED lamp (150 lumens) directed at the water surface at a 45 deg angle from ca. 20 cm away. Air and water temperatures during trials were 24±0.5°C.

We chose one focal segment of each ant video for measurement of leg stroke amplitude. The focal segment was selected based on three criteria: (1) all six legs were visible in the frame, (2) each leg completed at least three consecutive stroke cycles, and (3) ant motion was rectilinear. The focal video segment was converted to an image stack and the stroke amplitude of each leg was determined using the angle function in ImageJ. Stroke amplitude was measured as the difference between the minimum and maximum angle occurring between the apex of a leg and the midline of the thorax during a stroke (supplementary material Fig. S1). We also calculated the average stroke frequency (Hz) as the reciprocal of the duration of a complete stroke cycle. The duration of a stroke cycle was measured as the average number of video frames spanned by three to seven complete cycles for each ant. Stroke amplitude and duration data did not differ between right and left legs (paired *t*-tests, $P>0.77$), so we pooled paired leg data for a given ant and treated individual ants as independent units for analysis [e.g. data for right and left mid legs of an ant were combined to calculate a mid leg average for that ant (DuBois and Jander, 1985)].

We also qualitatively analyzed the high-speed videos described above to determine whether the ants conspicuously modify their gait for water surface locomotion. We followed basic protocols previously established for ants and spiders (DuBois and Jander, 1985; Suter et al., 2003). Specifically, we noted whether opposite legs in a pair moved in unison or asynchronously, and which legs contacted the water surface during different phases of a stroke cycle. We did not analyze the kinematics of our focal ants walking on solid substrates; however, our field observations showed that they employ the alternating tripod gait typical of ants walking on land (Zollikofer, 1994).

Directed swimming

We used the pool on BCI (described above) as an arena to test the hypothesis that swimming in *O. bauri* is directed at dark emergent objects (i.e. skototaxis). Workers of *O. bauri* were used for this experiment because they are diurnal, abundant and easily collected, and were among the fastest swimmers observed in preliminary trials (Table 1). A target consisting of a section of PVC pipe wrapped in a sheet of black high-density foam (final diameter=3.8 cm) was secured to the interior wall of the pool in a vertical orientation at a haphazardly chosen cardinal point (N, S, E or W). We dropped the ants following the protocol described above and relocated the target to a new cardinal point between trials. To determine whether the ants specifically swim toward dark objects rather than any emergent object, we repeated the experiment using a pipe wrapped in white foam, which was similar in appearance to the white interior walls of the pool. In all, 81 ants were dropped in three separate series of trials using the black target, and 96 ants in three separate series with the white target. Ants used in the experiment were collected from three different colonies and each ant was used only once. Water and air temperature ranged from 28.5 to 29.0°C and from 29.8 to 34.6°C, respectively.

Quantitative analyses

We tested for a phylogenetic signal in the distribution of swimming behavior using the *K*-statistic (Blomberg et al., 2003) calculated with the 'picante' package in R (R Development Core Team, 2008). We also tested for a relationship between gliding and swimming performance using phylogenetic generalized least squares analysis with a Brownian motion model using the 'geiger' package in R. We pruned the phylogeny of Moreau and Bell (Moreau and Bell, 2013) to 23 species representing the different ant genera for which we had both swimming performance and gliding performance data. For each genus, we used the average speed of the fastest swimming species (Table 1) and the average glide index for the best gliding species (Yanoviak et al., 2005) as measures of performance.

We used the Rayleigh test of uniformity (Fisher, 1993) to determine whether ants dropped onto the water at the ACTS site swam with a directional bias. This test measures the relative dispersion of data as a mean

vector *r*, which ranges from 0 (uniform distribution) to 1 (all data are on the same azimuth). We also used the Rayleigh test to determine whether *O. bauri* workers differentially direct their swimming toward emergent objects (the black or white targets) in the BCI pool. In this case, we normalized the position of the target as 0 deg for each trial to assess the effect of the target as an attractor regardless of its location.

Acknowledgements

Marilyn Feil and Benjamin Adams assisted in the field and contributed many useful ideas to this project. Comments from Robert Dudley, Evan Gora, Jeff Masters, Victoria Prescott and two anonymous reviewers improved the manuscript. We thank Pam Bucur and Stephen Madigosky for facilitating our research in Peru, and Oris Acevedo, Belkys Jimenez and the staff of the Smithsonian Tropical Research Institute for logistical support in Panama.

Competing interests

The authors declare no competing financial interests.

Author contributions

S.P.Y. conceived the study, collected data, interpreted the results, conducted analyses, and wrote the manuscript. D.N.F. designed experiments, collected data, interpreted the results and wrote the manuscript.

Funding

This research was supported by the National Science Foundation [IOS-0843120 and DEB-1252614 to S.P.Y.].

Supplementary material

Supplementary material available online at <http://jeb.biologists.org/lookup/suppl/doi:10.1242/jeb.101600/-DC1>

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