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Evidence of behavioral co-option from context-dependent variation in mandible use in trap-jaw ants (*Odontomachus* spp.)

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Abstract Evolutionary co-option of existing structures for new functions is a powerful yet understudied mechanism for generating novelty. Trap-jaw ants of the predatory genus *Odontomachus* are capable of some of the fastest self-propelled appendage movements ever recorded; their devastating strikes are not only used to disable and capture prey, but produce enough force to launch the ants into the air. We tested four *Odontomachus* species in a variety of behavioral contexts to examine if their mandibles have been co-opted for an escape mechanism through ballistic propulsion. We found that nest proximity makes no difference in interactions with prey, but that prey size has a strong influence on the suite of behaviors employed by the ants. In trials involving a potential threat (another trap-jaw ant species), vertical jumps were significantly more common in ants acting as intruders than in residents (i.e. a dangerous context), while horizontal jumps occurred at the same rate in both contexts. Additionally, horizontal jump trajectories were heavily influenced by the angle at which the substrate was struck and appear to be under little control by the ant. We conclude that while horizontal jumps may be accidental side-effects of strikes against hard surfaces, vertical escape jumps are likely intentional defensive behaviors that have been co-opted from the original prey-gathering and food-processing functions of *Odontomachus* jaws.

Keywords Foraging behavior · Locomotion · Competition · Prey capture · Defense · Formicidae

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Introduction

Biologists have long recognized that the evolution of new traits can arise from the co-option of existing parts for new functions (Jacob 1977), and that this sort of tinkering, using an ancient toolbox and limited number of spare parts, may be a primary source of biological novelty (Carroll 2005). These co-opted traits can range from novel functions for duplicated genes, seen in large, multifunctional 'gene families' derived from single progenitors (Holland et al. 1994; Guerrette et al. 1996; True and Carroll 2002) to physiological and structural novelties such as feathers for flight in birds (Prum 2005) and jaws in vertebrates (co-opted, modified gill-arches; reviewed

in Mallatt 1997). Behaviors that have evolved in one context can also take on new functions, as with aggressive male–male calls and movements that have been co-opted for courtship signaling in bowerbirds (Borgia and Coleman 2000).

A range of animal taxa, including stomatopods (Patek et al. 2004), anglerfish (Grobecker and Pietsch 1979), and "trap-jaw" ants (Gronenberg et al. 1993), have evolved suites of morphological and behavioral specializations for self-propelled, rapid attacks on prey. In ants, this is accompanied by remarkable diversification and specialization on a variety of prey types including fast-moving prey, such as springtails (Brown and Wilson 1959; Moffett 1985) and dangerous prey including other ants and termites (Ehmer and Hölldobler 1995; Dejean et al. 2002). In addition to reaching speeds in excess of 60 m/s, mandibles of trap-jaw ants in the genus *Odontomachus* can produce forces up to 400 times the ant's body weight (Patek et al. 2006; Spagna et al. 2008). Such high force production not only permits devastating strikes on prey, it can also result in intruders being pushed or thrown away from the nest, and allows the ants to "jump" into the air as a consequence of striking their jaws against a hard substrate (Wheeler 1922; Carlin and Gladstein 1989; Patek et al. 2006).

Observations of "jaw-jumping" in the genus *Odontomachus* have been known for some time (Borgmeier 1920; Wheeler 1922). However, it has recently been suggested that these behaviors may be purposeful rather than accidental consequences of extreme force generation. Thus trap-jaw ants may provide an example of the co-option of mandibles from prey capture and manipulation to a novel form of propulsion (Patek et al. 2006). Trap-jaw ants may therefore provide a powerful system with which to test hypotheses about the evolution of co-option and specialization.

Though jump and strike parameters have been measured in a variety of species (Patek et al. 2006; Spagna et al. 2008) and the neuromuscular physiology of the jaws and associated opening and closing muscles have been characterized in both *Odontomachus* (Gronenberg et al. 1993; Gronenberg and Tautz 1994; Gronenberg 1995a; Gronenberg 1995b; Gronenberg et al. 1998; Just and Gronenberg 1999) and other trap-jaw ant genera (Gronenberg, 1996; Gronenberg et al. 1998), less is known about how these capabilities, particularly the jump behaviors, play out in actual encounters with potential prey,

predators, or competitors. Previous behavioral studies have focused on inter-colony and interspecies recognition (Jaffé and Marcuse 1983) and description of prey detection and choice (Dejean and Bashingwa 1985; Dejean and Lachaud 1991) and largely ignore jumping behavior, or treat it as an accidental effect of misdirected strikes (Fowler 1980).

In this paper, we examine if mandible use for locomotion is context-dependent in the trap-jaw ant genus *Odontomachus*. Specifically, we examine the frequency in which different species exhibit a suite of behaviors (jaw-strikes, jaw jumps, and stings) in two contexts: the proximity of the forager to the nest and the size of prey encountered. We also track the rates of these behaviors during interspecific encounters between pairs of *Odontomachus* species, varying the context (intruder or colony resident) of the focal species. We use four species of *Odontomachus* that span much of the variation in body size seen in this genus (see Table 1), to examine possible effects of relative size on rates of behavior and to examine the generality of strike behaviors across the genus. Finally, to test the hypothesis that jump direction is determined by the relative position of the mandibles against the substrate, we varied the angle at which the ants strike a surface and used high speed video to track each ant's trajectory. These data provide insight into the context-dependent use of jaw-strikes in trap-jaw ants, allowing inferences to be made about the intentionality of the spectacular strikes and their ballistic consequences.

Materials and methods

Study organisms and behaviors measured

We collected colonies of four species of *Odontomachus* (two relatively small: *Odontomachus brunneus* and *Odontomachus haematodus* and two relatively large: *Odontomachus cephalotes* and *Odontomachus erythrocephalus*) and maintained them at 24°C in a controlled-temperature room with a 12–12 light–dark cycle. Species were selected from throughout their pan-tropical and subtropical distribution to cover a range of body sizes (Table 1).

Each laboratory colony consisted of a nest chamber contained within a rectangular foraging arena with dimen-

Table 1 Collection and size data for experimental colonies

Species—author	Locality	Body mass (mg)	Head width (mm)	Jaw length (mm)	Jaw mass (mg)
Odontomachus haematodus Linnaeus 1758	P.N. Iguazu, Argentina	6.0 (0.8)	1.60 (0.08)	1.16 (0.07)	0.056 (0.010)
Odontomachus brunneus Patton 1894	Florida, USA	7.6 (0.7)	1.79 (0.07)	1.16 (0.01)	0.070 (0.004)
Odontomachus erythrocephalus Emery 1890	La Selva, Costa Rica	12.7 (0.5)	2.20 (0.07)	1.58 (0.04)	0.144 (0.016)
Odontomachus cephalotes Smith 1863	Queensland, Australia	16.7 (2.1)	2.28 (0.13)	1.60 (0.05)	0.162 (0.003)

Values represent means; parenthetical values are standard deviations

sions 40-cm long by 26-cm wide by 10-cm deep. The nest chambers were made of covered, round plastic Petri dishes 14.5-cm diameter and 2-cm deep filled to approximately 0.5-cm depth with plaster of Paris. Holes in the sides and lids of the nest chambers allowed ants to move freely to and from the forging arena. Ants were fed a diet of crickets, tenebrionid larvae, and waxworms three times weekly, while water was made available ad libitum.

Though *Odontomachus* ants are capable of using their jaws for a full range of functions, including brood care and carrying prey, our behavioral observations were focused on those utilizing the extreme striking ability of the jaws. We also recorded stinging as it is often seen after a jaw-strike and thus was considered a potentially important part of the strike sequence. The behaviors tracked in each experiment are defined as follows:

Jaw-strikes—the ants triggered their jaws in a way that impaled, trapped, sliced, or "threw" a prey item or competitor.
Stings—following some jaw-strikes, the ants curled their abdomens under their body and stung their prey or competitor.
Bouncer-defense jumps—jaw strikes resulting in the ant being thrown backward away from the potential prey or competitor, with a more-or-less horizontal trajectory (Carlin and Gladstein 1989; Patek et al. 2006). These resulted from strikes with against an upright object, jaws oriented parallel to the ground. Depending on the experiment, this object could be another animal (cricket prey or another *Odontomachus* species) or a spatula introduced by the experimenter to control the angle at which the ant makes contact with the object.
Escape jumps—jumps resulting from the ant orienting its cocked jaws toward the ground before firing, launching it vertically (Patek et al. 2006). Only jumps that resulted from the ants orienting their jaws normal to the ground and then striking the substrate were classified as escape jumps, (whereas bouncer-defense jumps resulted from strikes against above-ground objects). Escape jumps were also typically preceded by the lifting of individual legs (Patek et al. 2006), which were visible in filmed jumps.

Experiments

We conducted three experiments to examine if the behaviors described above are context- or species-dependent. Evidence for context dependence of jumping behaviors provides support for the hypothesis that the ants purposefully use their jaws for propulsion (e.g. to avoid a threat). The contexts examined in the experiments included variation in the item encountered (small prey, large prey, or competitor/predator),

the location of the encounter (near the nest or away from the nest), and in the focal species of *Odontomachus* used. The unit of replication for each experiment is a "trial" defined as an independent observation of a focal ant interacting with a prey item or competitor/predator. However, because the ants were not marked, it is likely that individuals were used in more than one observation or experiment. All ants used for these experiments were selected from those moving about outside the nest chamber, as those performing nurse and guard tasks within the nest chamber might be expected to behave differently (Powell and Tschinkel 1999). Except where otherwise cited, statistics were performed using Statistica software (version 6.0, StatSoft, Tulsa, OK) and plots were produced using either Statistica or Excel 2003 (Microsoft, Seattle, WA).

Experiment 1A: Near-nest encounters In this experiment, two sizes of potential prey item, a large (mean mass 308 mg) or small (mean mass 9.40 mg) cricket was introduced into the foraging area of the experimental colony's nest and observed for 3 min. If an encounter with an ant occurred within the 3-min period, the ant's behavior upon first interaction was recorded (strike, sting, bouncer defense, or escape jump). If the cricket was not encountered by a worker within 3 min, the cricket was removed. We recorded rates of strikes, stings, and both jump types for 90 trials, for each cricket size, for each of the four trap-jaw ant species.

Experiment 1B: Changing context—away-from-nest encounters In these encounters, individual foraging worker ants were removed from the near-nest foraging area and placed in medium-sized Petri dishes (9-cm diameter, 1.2-cm deep) and allowed to acclimate for 5 min. A small cricket was then introduced into the dish with the single ant, and behaviors were tracked ($n=31–44$ encounters per species) as in Experiment 1A, except that the time limit for the first encounter was extended to 10 min to compensate for fewer ants being present to interact with the cricket. Large crickets were not introduced as they were too large for the smaller Petri dishes. Species data were pooled for statistical comparison due to the low frequency of the focal jump behaviors.

Experiment 2: Introduction of a competitor/predator Experiment 2 was performed in the same manner as Experiment 1 (3-min trials) except that a trap-jaw ant of another species was introduced into the near-nest area of the test colony rather than a cricket and the first behavior upon interacting was scored for both the introduced ant and the first resident ant to interact with it. Ants in the genus *Odontomachus* are highly predatory, are known to take other ants as prey, and are often aggressive to others ants

generally, making them suitable for this comparison (Carlin and Gladstein 1989; Ehmer and Holldobler 1995). The introduced species were *O. brunneus*, *O. erythrocephalus*, and *O. haematodus* and each was introduced into the nests of *O. erythrocephalus* and *O. haematodus*. Sixty trials were performed for each resident/introduced species combination, for four total combinations, as ants were not introduced into another colony of their own species due to the difficulty of visually tracking identical-looking workers during rapid interactions).

Experiment 2: Dependence of bouncer-defense jump angle on substrate angle To test the hypothesis that the trap-jaw ants can influence the trajectory of the bouncer-defense jumps (rather than uncontrolled "accidents" resulting from errant strikes against hard surfaces), we presented ants of three species (*O. erythrocephalus*, *O. haematodus*, and *O. brunneus*; $n=13$, 15, and 12, respectively) with a flat metallic chemistry spatula held at a range of angles. As is typical when foreign objects are introduced into a colony, the ants often snapped at the spatula, launching themselves into the air. Jumps were filmed at 500 frames s^{-1} against a vertical grid background, and the spatula angle and initial trajectory of the ant (relative to the bottom of the enclosure) were estimated in degrees manually from a single frame taken at the point that the thorax (the approximate center of mass) first passed the gridline 2 cm above the launch surface. Ordinary least-squares (OLS) regressions were used to determine the relationship between spatula angles and trajectories for each species.

Results

Experiment 1A: Near-nest encounters The full suite of strike behaviors, both types of jumps, strikes, and stings, was seen in all four species in the encounters in this experiment, with significant variations in frequency of the individual behaviors depending on prey size and ant species (Fig. 1). Pooled across species, the rarest events were the vertically oriented escape jumps, occurring in 4.7% of all encounters. Frequency of escape jumps was not related to prey size (15 total jumps vs. small crickets, 19 vs. large crickets, $\chi^2=0.47$, $P=0.49$), nor did it vary significantly by species ($\chi^2=6.7$, df=3, $P=0.08$). Frequency of bouncer-defense jumps was significantly influenced by both species ($\chi^2=13.86$, df=3, $P=0.003$) and prey size ($\chi^2=14.52$, df=1, $P<0.0001$), occurring nearly three times as often in the presence of large prey as with small prey (83 vs. 28 total jumps, respectively).

Prey-strikes resulting in the cricket being grabbed by the ant were the most common outcome across all species and both prey sizes, but were significantly more frequent with small crickets than with large crickets (245 vs. 73 total strikes, $\chi^2=93.83$, df=3, $P<0.0001$), with significant interspecific variation ($\chi^2=43.48$, $P<0.0001$). Stinging, as a follow-up to grabbing a potential prey item, also varied significantly by species ($\chi^2=61.65$, $P<0.0001$) and by prey size ($\chi^2=22.35$, df=1, $P<0.0001$), with *O. cephalotes* stinging following 78% of grabs and *O. brunneus* stinging only 33% of the time (Fig. 1). Large prey were nearly always stung following grabs (72 of 73 grabs were followed by stings), while smaller prey were only stung

Fig. 1 Frequency of first behavior (as % of total encounters, 90 trials per each cricket-size per species) seen in near-nest encounters for four species of *Odontomachus*, versus large and small crickets. *Error bars* represent one standard deviation
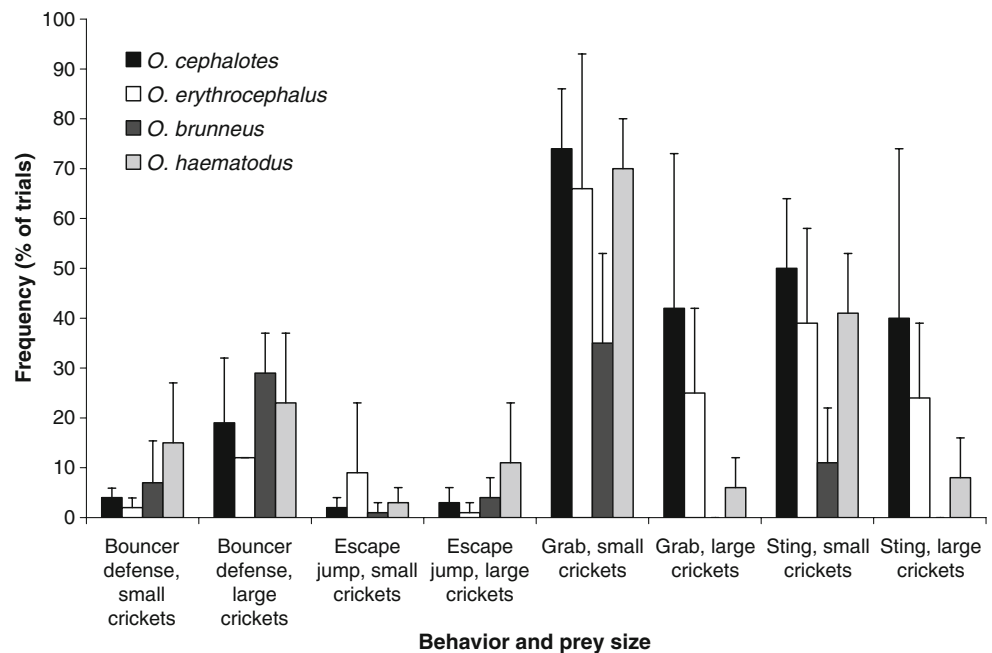
58% of the time (141 of 245 total grabs). In many trials, small prey impaled upon the ants' jaw tips were simply lifted off the ground and carried toward the nest chamber, with no sting required to disable the prey.

Experiment 1B: Away-from-nest encounters Comparing the rates of behaviors with small crickets near the nest (Experiment 1A) to small crickets away from the nest showed no significant differences in rates of the focal behaviors (bouncer-defense jump, escape jump, grab, and sting) relative to nest-proximity (χ^2=1.01, df=3, P=0.80; Fig. 2).

Experiment 2: Introduction of a competitor/predator into a colony's foraging area Introductions of a potential competitor/predator into the foraging arenas of other trap-jaw species resulted in differences in the relative frequencies of bouncer-defense jumps, escape jumps, and strike behaviors (Fig. 3). These did not vary significantly by species (P>0.05) with the exception of the vertical escape jumps (χ^2=6.0 df=2, P=0.049), which were performed most often by the small bodied *O. haematodus* (20% of encounters), and least often by the larger *O. erythrocephalus* (5% of encounters).

Across species, the frequencies of the focal behaviors differed based on whether the ants were near their own nest chamber or were introduced into the foraging area of another species. In general, ants were more aggressive near their own nests than when introduced to another colony's foraging area—striking and stinging 41% and 26% of the time respectively as residents, which they never did when acting as the intruder. By contrast, introduced ants were almost four times as likely to perform escape-jump maneuvers
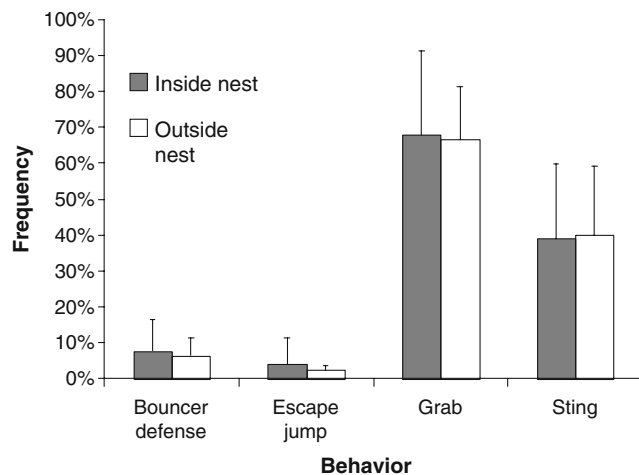

Fig. 2 Comparison of rates of initial behaviors in ant vs. cricket encounters in two behavioral contexts (near the nest and away from the nest). Data were not different among the ant species and are pooled for presentation. Differences in rates for all four behaviors did not differ significantly between the two behavioral contexts (P>0.05). *Error bars* represent one standard deviation
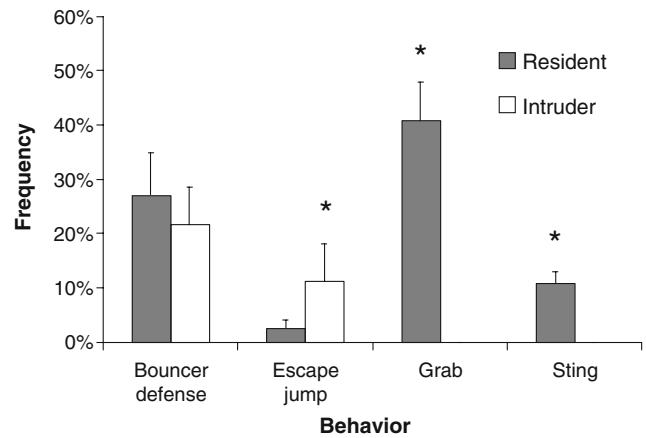

Fig. 3 Behavior of trap-jaw ants in a dangerous context—either near their nest when a competitor/predator is present (*resident bars*), or when placed near a colony of another species (*intruder bars*). With the exception of escape jumps (see text), data were not different among species and are pooled for presentation. Frequencies of escape jumps, grabs, and stings varied significantly between "resident" ants and "intruder" ants (P<0.01), significantly higher frequencies marked with an *asterisk*. There was no difference in frequency of "bouncer defense" jumps between resident and intruder ants. *Error bars* represent one standard deviation

as the near-colony ants (χ^2=13.4, df=1, P<0.001). There was no significant difference between near-colony and introduced ants' frequency of bouncer-defense jumps (χ^2=1.44, df=1, P=0.23).

Experiment 3 The relationships between the initial trajectory and the substrate angle were significant (P<0.001) and negative for all three species with r^2 values of 0.65, 0.70, and 0.70 for *O. haematodus*, *O. erythrocephalus*, and *O. brunneus*, respectively, indicating 65–70% of the variance in trajectory is due to the angle of the surface struck, with more upright surfaces resulting in more horizontal trajectories and flatter surfaces resulting in more vertical trajectories (Fig. 4). Comparing regressions yields significant differences in both slope and intercept between *O. haematodus* (intercept=97, 95% CI 75 to 119; slope=−1.02, 95% CI −0.6 to −1.4) and the other two species, but not between slopes nor intercepts of *O. brunneus* (intercept=67, 95% CI 56 to 77; slope=−0.60, 95% CI −0.79 to −0.42) and *O. erythrocephalus* (intercept= 63, 95% CI 50 to 77; slope=−0.54, 95% CI −0.76 to −0.31).

Discussion

The frequencies that trap-jaw ants in the genus *Odontomachus* use their jaws to strike prey or for ballistic locomotion is generally similar across a considerable range of body sizes in this genus, though previous work has shown considerable variation in force-production based on worker size (Spagna et al. 2008). However, the frequencies of these behaviors did
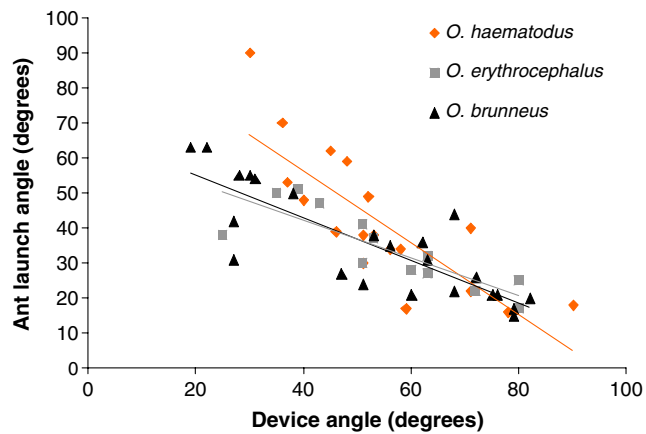
Fig. 4 Relationships between substrate angle and jump angle in bouncer-defense jumps in three species of *Odontomachus*. All regressions significant at the $P<0.001$ level

vary based on encounter type and proximity to the nest. When faced with potential prey, the workers of the four focal species performed the same behaviors at the same rates, with no evident regard for whether or not they are near their own nest chamber or in an unfamiliar (but not explicitly threatening) situation. In contrast, when faced with a potential competitor/predator, those near the nest acted aggressively (as evidenced by strike and sting behaviors) while intruders were more likely to exhibit jumping behaviors presumably to facilitate escape. The predominance of the strike over the sting as the primary aggressive behavior is consistent with the findings of De La Mora et al. (2008), where the rate of stinging is dependent on the prey type and stinging is often bypassed following successful strikes.

In Experiment 1, relative size of the prey animals involved appeared to influence the rates of the ants' behaviors. The smaller crickets were clearly easier to grab than the large ones (for all ant species), with one of the two smaller ant species (*O. brunneus*, mean mass 7.6 mg) never grabbing the large crickets. This is unlikely a result of physical limitation, however, as the smallest species (*O. haematodus*, mean mass 6.0 mg) did grab the large crickets, though at very low frequencies (6% of all encounters). *O. haematodus* was more likely to perform successful aggressive acts vs. the smaller crickets as well, grabbing and stinging twice as often (70%/ 41% vs. 35%/11% of encounters) as *O. brunneus*, suggesting that *O. haematodus* workers are generally the more aggressive of the two species.

Are jaw-jumps impressive accidents? The results of our experiments suggest that the horizontal "bouncer-defense jumps" (Patek et al. 2006) may most often result from strikes that happen to hit an unforgiving surface, rather than a purposeful attempt to propel the ant away from a prey item or competitor. While both types of jumps were rarer than non-propulsive prey-strikes, several observations

support the interpretation that at least a portion of the bouncer-defense jumps are accidents. First, bouncer-defense jumps are more common with large (but not particularly dangerous) prey than with small, harmless prey, but escape jumps are not (Fig. 1). The likelihood of being propelled backwards after a strike is also associated with the size of the striking ant—the smaller sized ant species (*O. brunneus* and *O. haematodus*) were most likely to propel themselves backwards off of a relatively large prey item. These results suggest that the launching backwards is the result of a non-penetrating strike on an essentially immovable object.

The results of the ant-versus-ant encounters also provide evidence that horizontal bouncer-defense jumps are not necessarily intended for escape as ants placed in proximity to other colonies ("intruders") show a greater tendency to perform escape jumps than the resident ants, but bouncer-defense jumps happen at approximately the same rate in both intruding and resident workers. The final piece of indirect evidence supporting the "impressive accident" scenario is that the ants appear to exert little control over the direction of bouncer-defense jumps, as the angles (and by extrapolation, the likely "flight distance") of these jumps are dependent on the substrate angle, and thus are somewhat dubious as effective defensive maneuvers. However, it should be noted that even if bouncer-defense jumps are by-products of extreme force production during a strike rather than purposeful escape maneuvers, ants can still benefit from their consequence if they are propelled away from a threat.

The difference in rates of vertical escape-jumps, in contrast, suggests that these are more likely "intentional" behaviors that may provide some defense for the ant. These jumps typically follow a series of behaviors (described in Patek et al. 2006) including lifting of one or more rear legs, followed by pointing the head at the horizontal surface before firing the jaws and shooting skyward, none of which are seen in the bouncer-defense jumps nor during prey-strikes, which suggest the behavior is not simply a variation on, or misplaced application of, another type of strike. Furthermore, the rate of escape jumps in Experiment 2 differs by species, with smaller intruder-ant species performing the jumps more often than larger ones. This would be consistent with an assumption that smaller ants are either under greater threat than larger ones when near another colony or can generate greater force with their jaws relative to their body mass (see Spagna et al. 2008). Grabbing and stinging behaviors are clearly influenced by distance to a nest chamber (one's own or another colony's), as grabs and stings were performed by the colony resident workers and never by the intruding workers. This context-dependent result is consistent with the finding of other studies where proximity to one's nest can influence the rate

of aggressive behaviors (Dejean and Lachaud 1991; Knaden and Wehner 2004). This provides evidence that we have produced a behavioral context that is explicitly dangerous for the intruding ant and the increased rate of escape jumps by intruding ants is consistent with the hypothesis that these are "intentional" defensive maneuvers.

The differences in rates of the two types of jumps (horizontal "bouncer-defense" and vertical "escape jump") in varied behavioral contexts from the present study, combined with ballistic evidence from previous studies, provides a strong case for treating these two types of jump as different behaviors, with different ballistic outcomes. While escape jumps do not propel the ant as far horizontally as bouncer-defense jumps (Patek et al. 2006), they do launch the ants vertically allowing them to grab onto the vegetation and other vertically oriented substrates (such as termite mounds, large rotten logs, and exposed roots) commonly found around their nests (authors' personal observations). The potential effectiveness of directional jumping with a large vertical component as a method of escaping lunging attacks from predators has been demonstrated in aquatic spiders, which use such jumps to successfully evade frog attacks (Suter 2003). Generally, the vertical jumps offer the advantages of requiring no contact with a potentially dangerous animal antagonist, nor contact with any other vertical elements, which may not be readily available in the immediate environment. More importantly, the relatively high frequencies of escape jumps in contexts where escape could actually be a lifesaving maneuver, requiring only a hard substrate to perform, supports the concept of the ballistic propulsion from jaw strikes as a fully co-opted, purposeful maneuver, and more aptly described as an adaptation than the bouncer-defense jumps.

Jaw-jumping as a case of evolutionary co-option Many cases of evolutionary co-option are complex—occurring at the levels of genotype, gene regulation, and development of phenotypic features and often require interactions between these factors (Arthur et al. 1999; Carroll 2005; Plachetzki and Oakley 2007). However, our results suggest that a relatively simple behavioral change (re-orientation of the jaw angle during an encounter with a dangerous foe) has given rise to a new function providing evidence that co-option of existing behaviors for new roles can be a common and powerful force in the evolution of novelty. In contrast to the simplicity of the behavioral modification required to adopt the novel function, understanding how selective pressures and evolutionary constraints act on the prey-strike and locomotor aspects of the system will be a challenge involving an integrated understanding of strike-force and speed production, vertical jumping ability, and ecological contexts (including prey and competitor species encountered in the field) in which the functions are actually used. Future work capitalizing on the variation in body size and ecology seen among species as well as the multiple origins of trap jaw morphology in ants will be essential for understanding the selective forces that promote the evolution of novel functions in this system.

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