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What can ants tell us about collective behavior during a natural catastrophe?

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Abstract The fire ant, *Solenipsis invicta*, has successfully invaded and colonized ecosystems worldwide. Like humans, fire ants build permanent domiciles to house family members, establish well-defined territories for foraging and fight to the death when invading neighbors breach the borders. One of the more striking behaviors of fire ants is their ability to form a living raft when springtime rains flood their domiciles. What are the survival benefits, if any, to collective behavior during a flood? To address this question, we quantified the survival of individuals as solitary swimmers compared to cooperative rafters. We found that large workers and matriarchs survived equally well as solitary swimmers or rafters. In contrast, small workers drowned whether they were solitary swimmers or rafters. However, when rafting with large workers or matriarchs, the mortality of small workers declined three-fold. We propose a behavior phenotype classification scheme to catalog the diverse behaviors observed in this series

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of experiments. Although the ultimate goal of rafting behavior by fire ant workers is to protect their matriarch, the proximate goal for the vast majority of fire ants is to save themselves first and to save others if the opportunity arises.

Keywords Self-organization · Division of labor · *Solenopsis invicta*

JEL Classification A13 · B49 · B59 · C72 · C91 · D63 · D64 · J16 · Z13

1 Introduction

In its simplest form, collective behavior is a group of individuals working together to achieve a common goal. Collective behavior has been a focal point of study in such diverse fields as philosophy (Tuomela 1995) social psychology (Stroebe and Frey 1982; Garrison 1992; Kelly and Breinlinger 1996; Wright 2003; van Zomeren et al. 2008, political science (Ostrom 2000; Olson and Olson 2009) and economics (Runge 1986; Tarrow and Tollefson 1994; Hirshleifer 1999, 2000; Sandler and Hartley 2001; Diani and McAdam 2003). Biology has taken a reductionist approach to understanding collective behavior by studying the mechanisms by which individuals initiate and complete tasks (Tinbergen 1953; Boyd and Richerson 1992; Kelso 1997; Cassill 2003; Karsenti 2008).

Insect societies, particularly ant societies, have been employed as surrogates for the study of collective behavior among humans (Cassill et al. 2007; Cassill and Watkins 2010; Czaczkes 2011; Grüter et al. 2012). Like humans, ants build permanent domiciles to shelter and protect mothers and their offspring (Hölldobler and Wilson 1990; Tschinkel 2006); ants process and distribute food among society members using a complex language (Cassill 2003); and, ants establish territories and to fight to the death when invaders breach the borders (Tschinkel 2006). Like humans, individual ants make decisions minute-by-minute about whether or not to engage in a task (Cassill 2003; Cassill et al. 2008, 2009). Indeed, ants have proven to be a rich system for gaining insights into collective action within corporations (Hill and Cassill 2004), governments (Allen and Cassill 2010) and even human families (Cassill 2002, 2003; Hardisty and Cassill 2010). With ant societies, robust experimental methods can be employed to answer cause-and-effect questions about survival/mortality that cannot be conducted legally or ethically with humans. Moreover, experiments comparing solitary effort to group effort can be addressed. Some might argue that ants do not engage in solitary pursuits. But in fact, they do. At any given time, 10–30 % of the population of worker ants in a colony is engaged in highly solitary tasks such as sleeping (Cassill et al. 2009), scouting for food or patrolling for invaders (Cassill 2003; Tschinkel 2006). Even their choice of tasks within the domicile is idiosyncratic as personalities and moods change with time, hunger and other variables (Cassill and Tschinkel 1999a, b).

One of the most striking examples of collective action in the fire ant, *Solenopsis invicta*, is the formation of living rafts during springtime floods (Fig. 1; Taber 2000; Tschinkel 2006; Mlot et al. 2011). The matriarch, her immature offspring (eggs, larvae and pupae), her fertile offspring (virgin sons and daughters), and her sterile offspring (the workers) are capable of staying afloat for weeks at a time until flood waters recede.

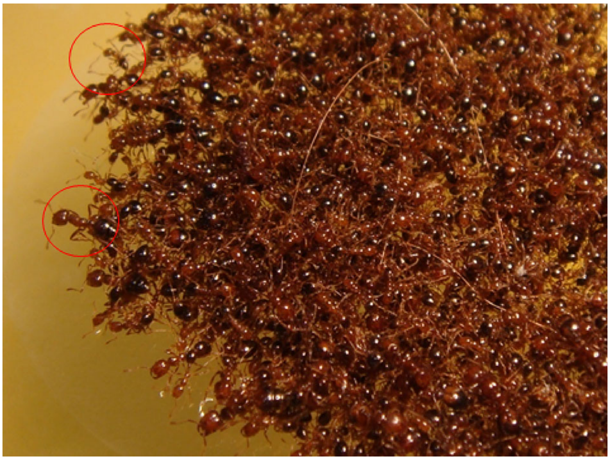

Fig. 1 Fire ant workers rafting in an artificial pond. The fire ant raft generally consists of two layers; a wet bottom layer composed of linked and immobile workers and a dry upper layer composed of mobile workers, the matriarch and her offspring. The *circles* indicate a large worker at the edge of the raft ready to latch onto anything solid such as a leaf or another ant; and a small worker that fills in the gaps between large workers. Note that most workers on the bottom layer at the edge of the raft face outward while those on the upper, inner layer face all directions. Photo by Alexander Casella

If an individual worker at the edge of the raft grapples onto a branch, leaf or grass stem along the shore, other workers quickly form bridges by grappling onto each other's bodies, allowing the matriarch and her offspring to exit the raft and return to land (Morrill 1974). Eventually, when flood waters recede, workers once again excavate a domicile in the damp soil, patrol for invaders and scavenge for food for the matriarch and her offspring.

In this study, we compared the ability of queens, large workers and small workers to survive as solitary swimmers or rafters. We then classified the individual cost-benefit of collective behavior relative to solitary behavior. By better understanding the survival/mortality of collective behavior among ants, we hope to improve our understanding of collective behavior among humans.

2 Methods

Mature fire ant colonies were collected during October 2010 and March 2011 from north Pinellas County, FL, USA and during May and June 2014 from east Hillsborough County, FL, USA. Colonies were separated from the soil (Banks et al. 1981) and maintained in artificial nests in an insectary at 27 °C and ~65 % relative humidity. The insectary was illuminated 24 h a day. Stock colonies were provided fresh water, 25 % sugar water, and frozen crickets three times a week. To determine their social form, polygyne or monogyne, workers from colonies collected at these sites were sent to a USDA molecular-testing lab in Gainesville, FL, USA. All colonies were confirmed as monogyne. For the experiments, small, medium or large workers were selected from a stock colony and then counted or weighed as a group. Ant workers were then placed in a paper cup and shaken to clump them into a ball. Thereafter, workers were gently added to the water. For experiments lasting 5 days, rafting workers were held in place with a needle imbedded it in a small lump of clay anchored to the bottom of the artificial pond. The needle's point was just above the water line so that only one or two workers could anchor to it. Droplets of water were added if needed to account for evaporation. In shorter experiments, rafts were moved by the observer back to the center of the artificial pond.

2.1 Raft size

Does the size of a raft affect individual survival? Four treatments were established. Number of workers per raft was as follows: solitary workers, small raft size (40 workers), medium raft size (0.3 g ~400 workers) and large raft size (1.5 g ~2,000 workers). Artificial ponds were constructed using plastic boxes ($15\,\text{cm} \times 15\,\text{cm} \times 5\,\text{cm}$) with water at the midpoint. After 3 days of rafting, workers were removed with forceps. The number of drowned workers was recorded (drowned ants were identified by their grossly swollen abdomens). Solitary swimmer treatments were replicated (20 small workers, 20 large workers, 20 fertile, virgin females). Small raft size was replicated 15 times; medium raft size was replicated 30 times and large raft size was replicated 6 times.

2.2 Body size

Does the size of workers forming a raft affect individual survival? Three treatments were tested: small workers ($N = 40$); large workers ($N = 20$); mixed-size workers ($N = 60$; 40 small + 20 large workers). At the end of 4 days, workers were removed from the artificial pond and placed on a paper towel. The number of drowned workers was recorded. Each treatment of small workers, large workers and mixed workers was replicated 10 times for a 3×10 experimental design.

2.3 Raft mergers

Do rafts from different colonies merge together? An artificial pond was constructed using a large bin ($1\,\text{m} \times 0.5\,\text{m} \times 0.15\,\text{m}$). The artificial pond was then filled half way with water. Three treatments were constructed: two rafts from the same colony, two rafts from next-door-neighbor colonies and two rafts from distant colonies collected 45 miles apart. Approximately 0.4 g workers (~500 workers) were collected to form each raft. Once rafts reached a stable conformation at the ends of the artificial pond, they were gently pushed together. The time for the two separate rafts to condense from an "8" shape into one oval or circular shape was noted. Each treatment was replicated 4 times for a 3×4 experimental design.

2.4 Raft cohesion

How do workers link to each other? A large artificial pond (as described above) with a sand island in the middle was constructed. Workers (1 g ~1,250 ants) were haphazardly selected and placed on the sand island. Water was slowly added until the group of ants was free-floating. Once a stable raft conformation had been reached, the raft was flash frozen using liquid nitrogen. The frozen raft was immediately transferred to a plastic container and placed in the freezer. The frozen raft was viewed under a microscope to determine general organization and the type of worker attachments holding the raft together.

2.5 Raft generation

One at a time, large workers ($N = 25$), small workers ($N = 25$) and matriarchs ($N = 22$) were dropped into an artificial pond from a height of 30 cm to determine whether they landed on their ventral or dorsal surface.

To determine initial raft formation, workers were added one or two at a time to a single, swimming matriarch until the matriarch was atop the workers. A total of 19 replicates was completed.

2.6 Raft degeneration

How do workers exit the raft? A raft of ~30 workers was established in clear plastic 15 cm petri dish with water to the halfway point. Once the raft was stable, a 20 cm wire bridge was placed at the raft's edge. The bridge led to a dry sand arena. The exiting workers were videotaped from above and below at ~10X magnification and then analyzed frame-by-frame to determine how workers exited the raft. Three replicates were videotaped simultaneously from the side and the bottom.

When does the matriarch exit a raft? Rafts composed of a mated queen and ~100 workers were established in an artificial pond (plastic box: 15 cm × 15 cm × 5 cm). Once a raft was formed and stable (~30 min), a wire bridge linked the raft of workers to a plastic box containing damp sand. The timing of the matriarch's exit was quantified as the percent of workers that had exited the raft before the matriarch made her exit. Sixteen replicates were completed.

2.7 Data analysis

Data were analyzed using the statistical software JMP 8 (Sall et al. 2001). Nonparametric tests were used to analyze skewed data; parametric tests were used to analyze data distributions that were independent and symmetrical with equivalent variance.

3 Results

3.1 Raft size

Raft size (group number) did not affect worker survival (Fig. 2; Kruskal-Wallis: $\chi^2 = 4.35$; $p = 0.225$). For solitary swimmers, survival depended on body size (Kruskal-Wallis: $\chi^2 = 28.24$; $p < 0.0001$); 97 % of solitary small workers drowned, 5 % of solitary large workers and solitary virgin females drowned. With their high body fat and waxy cuticles, solitary virgin females literally "walked on water."

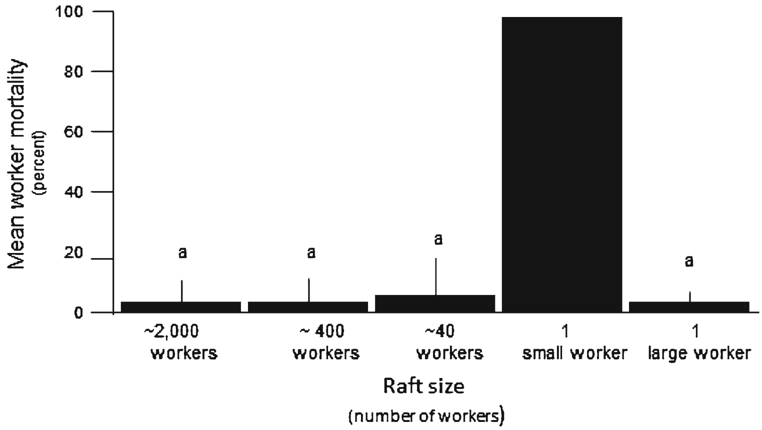

Fig. 2 Worker mortality by raft size. Worker mortality averaged 5–10 % regardless of raft size. Mortality for solitary swimmers depended on body size (virgin females not shown)

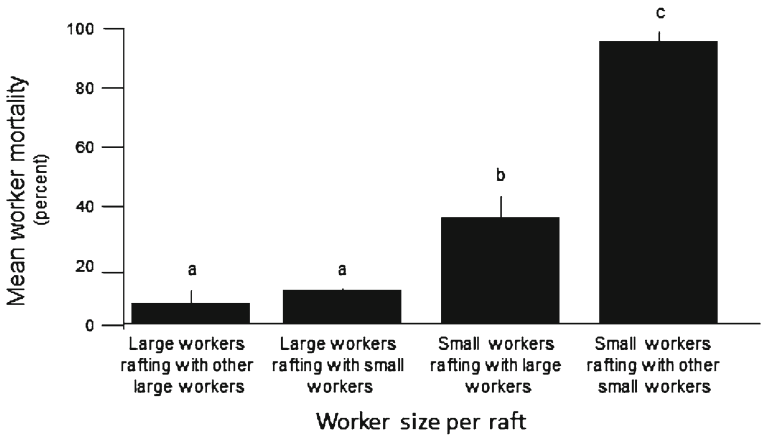

Fig. 3 Mortality based on body size. Small workers drowned in homogenous rafts but experienced significantly lower mortality when mixed with large workers. Large worker mortality was equally low whether they were in rafts with other large workers or mixed with small workers (N = 4 treatments × 10 replicates)

3.2 Body size

Body size of rafters significantly impacted worker mortality (Fig. 3; Kruskal-Wallis: $\chi^2 = 39.03$; $p < 0.0001$). Mortality was high when homogenous rafts were composed of small workers and low when rafts were composed of large workers. In mixed worker rafts, mortality for small workers was significantly reduced compared to homogenous rafts with small workers (Wilcoxon: $\chi^2 = 12.32$; $p < 0.0001$; 91–33 %). Because of their larger size and perhaps a thicker waxy cuticle, large workers were much less likely to be trapped by the water's surface tension and therefore had little difficulty surviving for days.

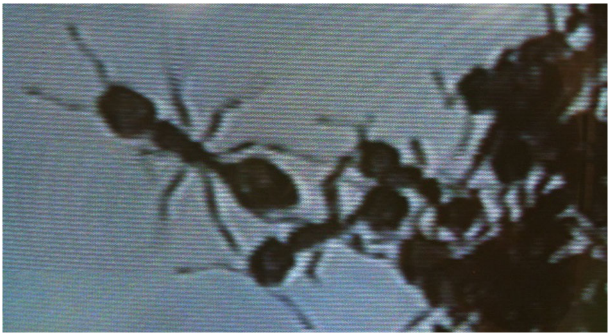

Fig. 4 Workers at the edge of the raft maintained contact with one or both hind-legs and paddled with the mid-legs and forelegs. Large workers were capable of swimming a small raft of workers to landfall. See video: http://youtu.be/NCUXFCN6qLE

Because matriarchs and larger workers could move from the bottom to the top layer with ease, the wet bottom layer was disproportionately composed of smaller workers. Large workers contributed by anchoring themselves to the edge of the raft with their hind legs and using their mid and forelegs to "swim" small rafts toward landfall (Fig. 4). Because larger workers were more often at the edge of the raft (Fig. 1), they were the first to anchor the raft to a leaf or a branch.

3.3 Raft mergers

There was a significant difference in the survival of rafting workers based on the level of aggression displayed when two rafts merged (Fig. 5; Kruskal-Wallis: $\chi^2 = 5.19$; $p < 0.0001$). Rafting workers from the same colony, or from next-door-neighbor colonies, joined without fighting. Rafting workers from distant colonies fought to the death with 100 % mortality in all four replicates. Agressive workers engaged in battle drowned within 20–40 min. Even large workers drowned as they bit and stung multiple intruders. Surprisingly, near-neighbor rafts merged 75 % more quickly relative to rafts composed of family members (t-test: $t = 3.89$; $p = 0.016$).

3.4 Raft cohesion

Workers linked themselves to other workers using jaws and claws (Fig. 6). Workers used their legs to weave themselves to other workers. Although jaws were used extensively to link to other workers, there was no evidence of damage or amputation of any body parts after workers made landfall. Apparently, workers are able to exert just enough pressure with their mandibles to hold their sisters without injury to either party.

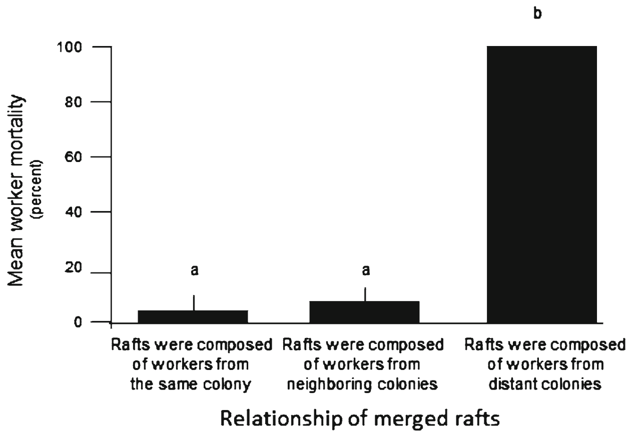

Fig. 5 Worker mortality within rafts that merged while afloat in an artificial pond. All colonies were of the monogyne social form (N = 3 treatments × 4 replicates)

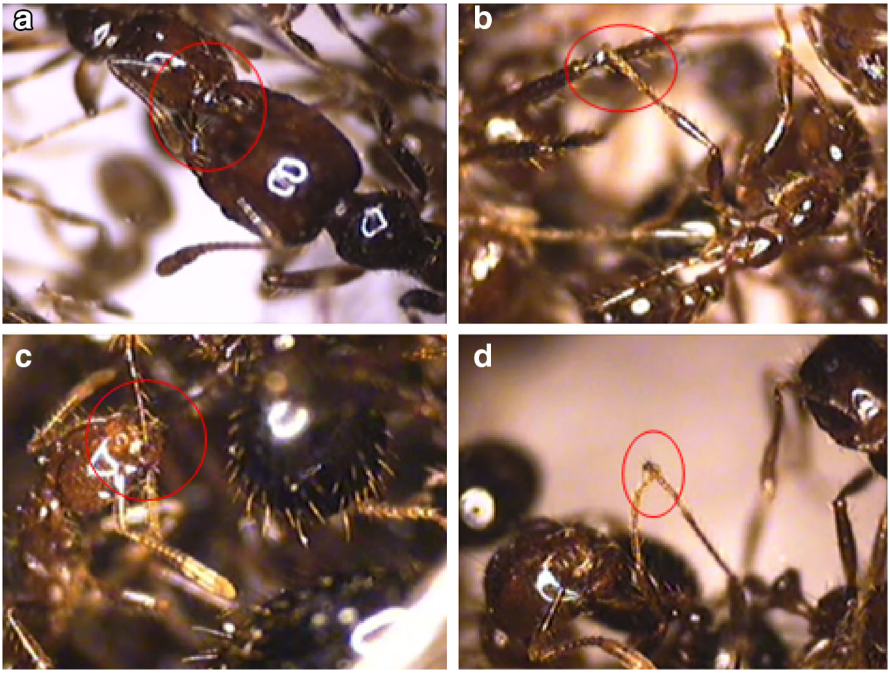

Fig. 6 Attachments between workers during rafting. **a** Workers grasped jaw-to-jaw. **b** Workers grappled foot-claw-to-leg. **c** Workers grasped jaw-to-leg. **d** Workers grappled claw-to-claw. Photos by Alexander Casella

3.5 Raft generation

Regardless of size, when individual workers were dropped onto water, 100 % landed on their ventral surface with legs spread out from the body; 100 % immediately began

Fig. 7 Histogram of worker size (J. Martin, unpublished data). Photo by S. Porter

to swim. Workers do not swim (or walk) in reverse; thus, each swam in the direction in which she had landed on the water. Even when two workers were close in distance to each other or to a floating leaf, workers would rarely change direction to swim to the other worker or to a leaf. Contact with another worker or a leaf occurred by chance alone. Occasionally, workers would pivot up to 45° at the waist and reach out to other workers. Whether or not the pivot was an intentional move to change direction was not obvious.

When the observer gently pushed workers together using forceps, large workers were such vigorous swimmers that, upon contact with their paddling legs, one would push the other away. In contrast, small workers stopped paddling upon contact and readily grappled onto large workers or each other with their claws. As the raft grew in size, interior workers remained in an unmoving, "spread-eagle" position, thus producing a relatively stable lower layer.

When as few as five to ten workers formed a raft, each grappled the others with back-legs or mid-legs but continued to face outward and paddle with mid-legs or forelegs. As workers were added to the raft, the core workers stopped paddling with the forelegs and latched onto the new workers with jaws or forelegs. Thus, each raft grew in a circular pattern at the edges as workers on the top layer walked to the edges and began to paddle when their forelegs touched the water's surface (Fig. 1). On the bottom layer, large workers functioned as stabilizers, much like spokes in a wheel; all faced outward with smaller workers filling the gapes in between the legs of the large workers. Because of their numeric superiority in colonies (Fig. 7), it was not surprising to find that the wet bottom layer of rafts was dominated by smaller workers. The orientation of workers, matriarchs and brood on the top layer was haphazard.

Occasionally, like an amoeba, one area at the edge of the raft grew at a faster rate than the other areas of the edge. The growth of a "finger" from the otherwise circular raft appeared to occur if there was a disturbance at that part of the edge. Perhaps an alarm signal rippled inward from the edge, activating workers on the upper layer to move to the edge.

To summarize, the wet bottom layer of the raft grew at the edges as large workers walked atop the bottom layer of small workers. When large workers touched water at the edge, they reached out, anchored themselves with their hind-legs and began paddling with the remaining legs. Small workers atop the bottom layer quickly filled the gaps between large workers by spreading all legs and connecting with whatever body part they touched (Fig. 1). As a consequence, most workers on the bottom layer faced outward with large workers functioning as stabilizing spokes on a wheel and small workers linking together to fill in the gaps between the spokes. The upper and top layers were unorganized with workers facing in all directions.

Unlike the workers, when individual matriarchs were dropped onto the water's surface, the majority landed on their side (14/22 = 64 %) or dorsal surface (6/22 = 27 %) with only two (9 %) landing on their ventral surface. When landing on their side, matriarchs rolled onto their ventral surface within seconds (range = 1–7 s) by extending the fore and mid-legs out and upward to pull against the viscous water. Once on their ventral surface, matriarchs began swimming. When landing on their dorsal surface, matriarchs struggled to right themselves (range = 28–356 s). Matriarchs curled forward with her thorax, head and legs out of the water such that their bodies took on a "C" shape. On average, ten workers ($\pm$1.0 SE) were needed for the matriarch to move from the bottom to the top layer of the raft. Initially, individual workers crawled atop the matriarch or latched onto her legs. As more workers were added, they formed a single layer until the matriarch was supported atop this layer.

3.6 Raft degeneration

The first to exit the raft were large workers on the dry top layer of the raft, facing the bridge. Once workers were on the bridge, a few workers continued over and into the dry arena. Others walked back and forth from the raft to the top of the bridge, laying a trail and actually returning to the raft to recruit other workers off the raft until only the wet bottom layer of workers was left. Bottom-layer workers anchored to the bridge with their back legs and, holding onto other workers with their jaws or front legs, would not exit the raft. Nor did workers leave a raft if three or more body parts are attached to other workers. Workers at the edge of the raft with only two back legs attached to other workers or to the bridge would eventually pivot on one attached back leg and climb up from the wet layer onto the backs of the remaining workers or onto the bridge. Thus, the raft was disassembled from the top layer first (the layer with the matriarch and brood), and then from the outer edges of the wet, bottom layer (Fig. 1). The last workers to leave were those on the bottom layer but closest to the bridge's surface. The time it took for all workers to exit the raft was approximately 2 h (mean = 119 min; range = 64–191 min. The matriarch exited at a mean 29 min (range = 2–46 min) with fewer than half the workers exiting ahead of her (range = 14–47 %). The timing of matriarchs leaving a raft was telling. A matriarch leaving a raft too soon would be vulnerable to desiccation or predation on land; a matriarch leaving too late would be vulnerable to being washed away, leaving behind the majority of her labor-force.

4 Discussion

We discuss our findings on collective behavior during raft formation by the fire ant, *S. invicta*, from several perspectives. From a self-organizing perspective, we found that, although no single worker possessed a blueprint of raft formation or composition, thousands of "diverse" individuals accomplished raft formation with a few, simple rules-of-thumb: If my feet are wet, spread my legs and paddle. When paddling, grapple onto the nearest object when it presents itself (the nearest objects for most fire ants during springtime floods are other ants). If more than three appendages are attached to others, do not move.

To account for the diverse survival outcomes, we developed a classification scheme (Table 1) that specifies the cost-benefit to an actor (self) and a passive recipient (other) based on an actor's decision to interact or not to interact with a passive individual.

How did survival outcomes of our experiments with rafting fire ants fit into the behavioral classification scheme? The survival outcomes of large workers and queens were classified as Behavioral Phenotype 1; both survived equally well as solitary swimmers or rafters. Survival outcomes for small workers were Behavioral Phenotype 16; the vast majority died whether they were solitary swimmers or rafters. However, when rafting with large workers, the survival outcomes of small workers were Behavioral Phenotype 6; small workers were three-fold more likely to survive when rafting with large workers than as solitary swimmers. Survival outcomes for a small portion of small workers rafting with large workers were Behavioral Phenotype 8; these individuals died despite rafting with large workers. The important point here is that, from a proximate perspective, none of the survival outcomes was classified as altruistic (Behavioral Phenotype 10 or 11).

Although fire ant workers and queens did not have a "choice" in our experiments, the assumption of choice allowed us to account for diversity among actors during collective behavior. For example, a mother might make one choice if the "other" is her offspring and a different choice if the "other" is an adult neighbor or a stranger. An assumption of equality leads to predictions that have limited generalizability or ability to solve the evolution of collective behavior.

From a political–economic perspective we found that, when compared to aggression, cooperating with near-neighbors was a superior survival strategy for workers and queens. Cooperative rafters survived; aggressive rafters died. These findings suggest that social networking at the edge of territories breeds tolerance during periods of stable conditions; and that tolerance increases survival during periods of unstable conditions.

In conclusion, what can ants tell us about collective action? Our findings on rafting in the fire ant, *S. invicta*, reveal that a queen's survival during a natural catastrophe depends on workers who help themselves first and help others when the opportunity presents itself (see also Cassill et al. 2011). Diverse physical and behavioral phenotypes between leaders and workers and among workers themselves are essential ingredients to successful collective action. In the fire ant, large workers function as homeland security within the domicile to protect the queen and her immature offspring from natural disasters such as flooding or invasion of the domicile (Cassill and Tschinkel 1999a, b). Because small workers are more numerous, they are more dispos-

Table 1 Survival/mortality behavioral phenotypes

Behavioral phenotype	No interaction	Interaction
Self	+	+
Other	+	+
1	Indifferent	Loyal
	Self survives; other survives	Self survives; other survives
Self	+	+
Other	+	−
2	Compassionate	Competitive, vindictive
	Self survives; other survives	Self survives; other dies
Self	+	−
Other	+	+
3	Self-interested	Irrational, idealistic, fanatic
	Self survives; other survives	Self dies; other survives
Self	+	−
Other	+	−
4	Self-interested	Irrational, fatalistic
	Self survives; other survives	Self dies; other dies
Self	+	+
Other	−	+
5	Spiteful	Heroic, loyal
	Self survives; other dies	Self survives; other survives
Self	−	+
Other	+	+
6	Irrational, fanatic, martyr	Ambitious, self-interested
	Self dies; other survives	Self survives; other survives
Self	−	+
Other	−	+
7	Irrational, fatalistic	Rational, mutualistic
	Self dies; other dies	Self survives; other survives
Self	−	−
Other	+	+
8	Indifferent victim	Loyal victim
	Self dies; other survives	Self dies; other survives
Self	+	+
Other	−	−
9	Lucky, Indifferent	Lucky, Loyal
	Self survives; other dies	Self survives; other dies
Self	+	−
Other	−	+
10	Self-interested	Altruistic loyalty

Table 1 continued

Behavioral phenotype	No interaction	Interaction
	Self survives; other dies	Self-dies; other survives
Self	−	+
Other	+	−
11	Altruistic	Self-interested loyalty
	Self-dies; other survives	Self survives; other dies
Self	−	+
Other	−	−
12	Irrational, fatalistic	Self-interested, loyal
	Self dies; other dies	Self survives; other dies
Self	−	−
Other	−	+
13	Spiteful, indifferent	Heroic, loyal
	Self dies; other dies	Self dies; other survives
Self	−	−
Other	+	−
14	Heroic	Spiteful, vindictive
	Self dies; other survives	Self dies; other survives
Self	+	−
Other	−	−
15	Ambitious, self-interested	Fatalistic, loyal
	Self survives; other dies	Self dies; other dies
Self	−	−
Other	−	−
16	Indifferent victim	Loyal victim
	Self dies; other dies	Self dies; other dies

The behavioral classification scheme assumes that "self" has the choice to interact or not to interact with a passive "other." In addition, the classification scheme assumes that the choice made by "self" will depend on the relationship between the two actors. In other words, the diverse demographics of each actor must be accounted for (gender, size, age, ability, personality, mood, etc.). Behavioral phenotypes are numbered; the nominal labels are suggestions that can be modified depending on the relationship of the individuals to each other. Quantifying non-interactive behavior and its outcome is an essential control when studying collective behavior (Cassill et al. 2007). Behavior phenotypes 1 and 16 are null hypotheses; i.e., there is no difference in the survival outcomes between interacting and not interacting. *Key* + survive; − die

able (Cassill 2002). Most high-risk jobs outside the domicile such as trail excavation, foraging/hunting/scavenging, patrolling and fighting are completed by small workers (Tschinkel 2006). In the final analysis, the lessons learned from the ant are that diversity and cooperation are essential ingredients for surviving complex environments (Cassill and Watkins 2010).

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