Behavioural Processes 119 (2015) 14–21

Contents lists available at ScienceDirect

Behavioural Processes

journal homepage: www.elsevier.com/locate/behavproc

Warring arthropod societies: Social spider colonies can delay annihilation by predatory ants via reduced apparency and increased group size

Carl N. Keiser*,[1], Colin M. Wright[1], Jonathan N. Pruitt

Department of Biological Sciences, University of Pittsburgh, Pittsburgh, PA 15260, USA

ARTICLE INFO

Article history:
Received 25 January 2015
Received in revised form 1 July 2015
Accepted 10 July 2015
Available online 20 July 2015

Keywords:
Anoplolepis custodiens
Group apparency
Group size
Stegodyphus dumicola
Predation risk

ABSTRACT

Sociality provides individuals with benefits via collective foraging and anti-predator defense. One of the costs of living in large groups, however, is increased apparency to natural enemies. Here, we test how the individual-level and collective traits of spider societies can increase the risk of discovery and death by predatory ants. We transplanted colonies of the social spider *Stegodyphus dumicola* into a habitat dense with one of their top predators, the pugnacious ant *Anoplolepis custodiens*. With three different experiments, we test how colony-wide survivorship in a predator-dense habitat can be altered by colony apparency (i.e., the presence of a capture web), group size, and group composition (i.e., the proportion of bold and shy personality types present). We also test how spiders' social context (i.e., living solitarily vs. among conspecifics) modifies their behaviour toward ants in their capture web. Colonies with capture webs intact were discovered by predatory ants on average 25% faster than colonies with the capture web removed, and all discovered colonies eventually collapsed and succumbed to predation. However, the lag time from discovery by ants to colony collapse was greater for colonies containing more individuals. The composition of individual personality types in the group had no influence on survivorship. Spiders in a social group were more likely to approach ants caught in their web than were isolated spiders. Isolated spiders were more likely to attack a safe prey item (a moth) than they were to attack ants and were more likely to retreat from ants after contact than they were after contact with moths. Together, our data suggest that the physical structures produced by large animal societies can increase their apparency to natural enemies, though larger groups can facilitate a longer lag time between discovery and demise. Lastly, the interaction between spiders and predatory ants seems to depend on the social context in which spiders reside.

1. Introduction

The evolution of sociality has afforded group-living predators ample benefits, including advantages gleaned by cooperative hunting (e.g., Lührs et al., 2012; Boesch 1994; Creel and Creel, 1995) and anti-predator defenses via increased group vigilance (Roberts, 1996 e.g., the 'many eyes' effect; Powell, 1974). Thus, sociality undoubtedly plays a major role in mediating countless predator-prey interactions in nature. Arguably some of the most spectacular species interactions that animal groups experience arise when societies collide. Examples of these have been documented for over a century; for example, intergroup combat between chimpanzee troops (Goodall et al., 1979; Wilson et al., 2002, mass-attacks by Vespid wasps decimating honey bee colonies (Matsuura 1988), and the "legendary" wars between insect societies like carpenter ants (Fielde et al., 1904) and wood ants (Elton 1932; Wallis, 1962). In fact, eusocial Hymenoptera have served as models for inter-group contests for over a century, even for testing principles of human combat (i.e., Lanchester's "laws of combat"; Whitehouse and Jaffe, 1996). Given that animal societies often require abundant resources to persist, they must exhibit diverse lines of defenses across multiple organizational scales to protect those resources from other societies and to defend themselves from predatory social groups.

For many social units, simple dilution effects (Foster and Treherne, 1981), selfish herd dynamics (Hamilton, 1971), or early warning effects (i.e., the "Trafalgar effect"; Treherne and Foster, 1981) reduce predation risk for individuals despite an increased

* *Corresponding author at: 213 Clapp Hall, 4249 Fifth Avenue, Pittsburgh, PA 15260, USA.
E-mail address: cnk21@pitt.edu (C.N. Keiser).
[1] These authors contributed equally to this work and are the co-first authors.

http://dx.doi.org/10.1016/j.beproc.2015.07.005
0376-6357/

encounter rate with predators (Mooring and Hart, 1992). For example, larger groups of the colonial spider *Metepeira incrassala* experience increased encounter rates with predatory wasps, though per capita predation risk decreases with group size via early warning effects (Uetz et al., 2002). Because these colonial spiders live in three-dimensional colonies, the surface area to volume ratio of colonies decreases as they grow, allowing individuals to escape predation at centrally located sites (Rayor and Uetz, 1993) and thus, predation risk scales non-linearly with group size (Uetz and Hieber, 1994). While the biomaterials produced by many animal societies (i.e., termites, wasps, social spiders) offer survival advantages, we argue that they might also increase the group's apparency to natural enemies in the same way that large, long-lived plants are 'bound to be found' by herbivores (Feeny, 1976).

Just like Feeney's (1976) plant apparency hypothesis, which predicts that plants that are more "apparent" to their herbivores should invest broadly in functional defenses, so too should animal societies with conspicuous architecture exhibit more complex defenses against their enemies. For example, dynamic social groups like fish shoals often exhibit intricate collective anti-predator escape behaviours (Hall et al., 1986) and social groups of red colobus monkeys live in larger groups and exhibit specialized defensive behaviours when in proximity of predatory chimpanzee troops (Stanford, 1995). But, how do high-apparency animal societies which live in stationary, perennial physical structures (e.g., most arthropod societies) survive in predator-dense habitats, and what collective anti-predator mechanisms mediate their survival?

Evidence from multiple gregarious or social arthropods suggests that smaller domiciles can allow groups greater survivorship by evading detection by predators (gregarious spiny lobster: Eggleston and Lipcius, 1992 social spider mites: Mori and Saito, 2004). Thus, domicile size and colony traits jointly determine predation risk in some diverse social groups. Two collective traits in particular may likely decrease the risk of mortality for high-apparency groups in predator-dense habitats: increased group size (i.e., a dilution effect) and achieving the appropriate phenotypic composition within the group. For example, predation risk can be decreased by the presence of leaders in elephant herds and fish dyads (Milinski et al., 1997; McComb et al., 2011) and groups of social spiders and ant colonies containing more aggressive individuals can thwart invasion by social parasites (Pruitt, 2013; Pamminger et al., 2012). Here, we test how three collective traits (colony apparency, group size, and colony behavioural composition) jointly influence colony mortality in regards to predation by a voracious social forager.

Stegodyphus dumicola is a social spider that lives in groups of up to several hundred individuals in arid Southern Africa. These social spiders are philopatric, living in long-term colonies which can last several generations. They live in colonies that consist of two main physical units: a three-dimensional silken retreat labyrinthed with tunnels where the spiders spend the majority of the day, and a large two-dimensional capture web which radiates from the retreat. These colonies experience strong top-down pressure from *Anoplolepis* spp. ants, causing up to 90% colony extinction rates in some populations in the Namib desert (Henschel 1998). Predation events on *S. dumicola* colonies are characterized by a sequence of events where one or a few scout ants discover the colony, more individuals are then recruited to the raid, and the workers tear apart the capture web and retreat silk to retrieve the spiders inside (Fig. 1). In response to an ant raid, spiders either evacuate the colony or begin to produce a defensive layer of cribellate silk to block the entrance of ants (Henschel, 1998). As opposed to the non-linear scaling of group size and colony size in the colonial spider *M. incrassala*, capture web size in *S. dumicola* appears to scale linearly with group size (Keiser and Pruitt, 2014). Thus, web apparency and predation risk might similarly increase linearly with group size in these spider societies.

Although the ant *A. steingroveri* will attack *S. dumicola* colonies of any size, multi-individual colonies are more likely to be discovered than individuals which are living solitarily (Henschel, 1998). Further, ant raids on *S. dumicola* nests are less common in populations where more *S. dumicola* live solitarily (Henschel 1998). Given the observation that some spider colonies appear to persist for many years in proximity to aggressively foraging *Anoplolepis*, we aim to identify the collective traits and individual behavioral mechanisms that allow some colonies subsist/linger while others are destroyed.

Here, using three different experiments, we address the following four hypotheses: (1) colonies whose physical structures are larger and, thus, more apparent to top predators will have decreased survivorship, (2) larger groups will have increased survivorship, perhaps due to dilution effects, (3) colonies containing more bold individuals (a "proactive" behavioural phenotype important for foraging in these societies) will have increased survivorship, (4) the behavioural interactions between predatory ants and spiders will differ between solitary individuals and social groups (i.e., their social context).

2. Materials and methods

2.1. Field site and study species

Colonies of *S. dumicola* were collected in February 2014 along roadside fences near Upington, South Africa (S28°27′24.9″ E21°24′09.0″). All three experiments took place in an arid thornveld near Griekwastad, Northern Cape, South Africa (S28°54′32.0″ E23°24′33.7″). This habitat was dominated by *Acacia mellifera* trees, similar to the sites where the spider colonies were originally collected. However, this particular site contained an abundance of an aggressive, ground-nesting predatory ant, *Anoplolepis custodiens*. This site contained 2–8 nest entrances per m^2 near *Acacia* trees and pitfall traps indicate that >95% of the insects surveyed were *A. custodiens*. Sites where spiders were collected, however, contained approximated 85% fewer *A. custodiens* during pitfall trap collections. These ants are voracious diurnal foragers (Addison and Samways, 2000; Löhr, 1992) and, although they exist in sympatry with *S. dumicola*, large spider colonies are rarely found at sites that contain high densities of *A. custodiens* (Henschel 1998).

2.1.1. Web apparency and group size

We collected 16 different source colonies ranging in size from 4 to 200 individuals, and divided each colony into two groups of equal size, each in a 240 ml clear plastic cup containing a piece of an *Acacia* branch to facilitate web construction. These cups are an appropriate volume for *Stegodyphus* colonies surveyed in the field containing these group sizes (Pruitt et al., 2013). Spiders from different source colonies were not mixed in attempts to preserve natural levels of within-group familiarity (Schneider and Bilde, 2008; Modlmeier et al., 2014). This provided us with 36 colonies, ranging in size from 2 to 100 adult female spiders. Experimental groups were allowed 24 h to produce a retreat in their cup before they were fastened to a branch of an *A. mellifera* tree with two clothespins at 8pm. This time-frame for retreat construction does not alter the survivorship of artificial colonies in this habitat compared to those that are allowed up to one month to do so, and all of these retreats perform about as well as naturally-occurring retreats that can be more than a year old (*unpubl. data*). Every colony built a capture web overnight (avg. web area: 1486 $cm^2 \pm 255$) and thus contained the two functional units of *Stegodyphus* colonies: a 3-dimensional retreat and a large 2-dimensional capture web. No more than three colonies were placed on a single tree, with at least 2 m between each colony, and we did not observe colonies constructing capture webs that were in contact with each other (i.e., "polydomous" colonies).