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Group foraging in the colonial spider *Parawixia bistriata* (Araneidae): effect of resource levels and prey size

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In animal groups whose focus is on juvenile growth, prey attributes and the way in which individuals have access to those prey influence the level of sociality. Models examining the evolution of group foraging predict that, if an individual is able to monopolize a prey item, it should not permit collaboration in the capture of or feeding on that prey. If monopoly is not possible, individuals should allow others to join because of the high cost of prey defensibility. Hunger stress can affect the above predictions through its effect on the perceived value of a prey item. An increase in the individual tendency to attack prey could result in more group captures at higher hunger levels when the resident spider fails to monopolize a prey item. I conducted a study on the foraging behaviour of the colonial spider *Parawixia bistriata* in habitats with different insect availability. I offered prey items of known size to spiders at their web sites and determined frequency of group capture and feeding relative to prey size. I also recorded the number of individuals participating in capture and feeding groups and interactions between the resident and other foraging spiders. Individuals showed a higher tendency to capture prey and feed in a group as the size of the prey increased. In addition, spiders from habitats with lower levels of prey (dry sites) had a higher tendency to attack prey collectively than did spiders from wet sites where prey levels were higher. Although there were no between-habitat differences in tendency to feed in groups, group sizes of foraging spiders were larger at dry sites. Levels of aggression between the resident and other foraging spiders were low over all trials, but behavioural acts involving direct interactions were more frequent in groups from dry sites.

Keywords: colonial spider; foraging; geographical variation; *Parawixia bistriata*; resource distribution; social behaviour

In social species, interactions among members of the group can have a preferential impact on different life stages of individuals, such as reproduction or juvenile growth. Thus, it is possible to classify animal groups into breeding societies and foraging societies (Whitehouse & Lubin 2005). In breeding societies, most social activities are associated with securing reproduction and the rearing and protection of offspring (e.g. social Hymenoptera: Keller & Reeve 1994; cooperatively breeding birds and mammals: Jennions & Macdonald 1994). Foraging societies, in contrast, are primarily influenced by foraging constraints, and most social activities within these groups affect individual growth (e.g. foraging, thermoregulation: Costa & Pierce 1997). Factors related to food acquisition, such as the risks involved in obtaining access to food, the methods used to catch and distribute prey among group members, and the procedures involved in handling or consuming the food could affect the level of cooperation or social interactions within the group (Whitehouse & Lubin 2005).

Colonial spiders are a group of social species of spiders that constitute foraging societies (Whitehouse & Lubin 2005). Colonial spiders produce many young and lack maternal care, and characteristics of the group are dominated by interactions during foraging. All colonial spiders are orb-weavers. Individuals are aggregated in colonies that are formed by the individual capture webs attached together by means of communally built framelines (D'Andrea 1987; Avilés 1997; Uetz & Hieber 1997). The individual capture webs are the territories defended from other individuals within the colony. Spiders usually forage solitarily on their capture webs, although they can steal food from others. Individuals may benefit from an

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increase in individual food acquisition indirectly, as a consequence of web grouping, when insect prey that escape from one web are deflected onto others ('ricochet effect'; Uetz 1989) or by enabling spiders to take advantage of prey-rich web sites that are unavailable to solitary individuals (e.g. gaps between trees; Lubin 1974; Sandoval 1987). Group foraging is absent in most colonial species.

Web mechanics are the main argument proposed for the lack of group foraging in colonial species (Lubin 1974; Buskirk 1975a, b; Krafft 1979; Rypstra 1979). The poor communication of prey-induced web vibration is less effective across a colony consisting of individual webs than across a colony that constitutes a single, large capture web (Lubin 1974). Interestingly, colonial spiders that move between webs to capture prey and that show the greatest degree of group behaviour are those whose webs are joined to form continuous sheets (e.g. *Parawixia bistriata*: Fowler & Gobbi 1988; de Carvalho 1998).

Parawixia bistriata (Araneidae) individuals regularly engage in group capture and prey sharing. This species seems to have overcome the constraints imposed by the web to other colonial species and provides a unique opportunity to examine the features that may have allowed it to overcome these constraints. This species shows facultative group foraging. Individuals forage in groups only when the prey is larger than the spiders involved, otherwise they forage solitarily. This variability in capture behaviour may be facilitated by the fact that spiders can move quickly from one web to the next, because the orbs are placed within a single plane, forming an extensive sheet of capture webs.

The occurrence of group foraging can be affected by ecological factors such as the size of the prey items and the levels of prey available. First, the size of the prey can affect the likelihood of group capture by affecting the chances of monopolization of the item. Packer & Ruttan (1988) developed a series of models that incorporate payoffs to analyse the circumstances under which it is advantageous to forage collectively or solitarily depending on prey size. One of the predictions of the model is that, if a prey item is small enough to be monopolized by a single captor, the predator should capture prey solitarily. Because large prey items are difficult to monopolize, the occurrence of group capture could increase with prey size when the benefits of a joint capture outweigh the disadvantage of dividing the prey. These benefits can be represented by an increase in capture success or a decrease in the costs involved in the capture and subduing of a prey item: larger prey items can be riskier and more difficult to catch and demand more venom and enzyme investment to subdue and digest (Ward & Enders 1985).

A second factor that could affect the tendency of individuals to participate in group foraging is hunger level. Hunger stress increases the perceived value of a prey item and an individual's willingness to accept the risks and energy expenditure associated with prey capture (Riechert & Luczak 1982; Lubin & Henschel 1996; Ainsworth et al. 2002). Thus, in colonial spiders, hungrier individuals could show a higher tendency to attack prey, including items caught in a neighbour's web. For a resident spider, this can increase the investment in defence of prey landing on its web. When residents try to maintain exclusive access to a prey item, it could result in aggressive interactions between neighbours. In addition, depending on the success of the resident spider at monopolizing the prey item, it could also result in more individuals participating in a capture (i.e. larger capture groups when prey is not monopolized by the resident spider).

I examined group prey capture behaviour of populations of *P. bistriata* from habitats with different resource levels. I compared the degree to which group foraging was related to food availability. I evaluated: (1) whether the strength of the tendency to forage in a group and the number of individuals participating in those groups increases with prey size and hunger stress; and (2) whether levels of aggression between the resident spider and neighbours participating in group foraging are higher in colonies under low prey conditions.

METHODS

Study Species

Parawixia bistriata (Araneidae) is a Neotropical colonial spider. Individuals defend their capture webs from conspecifics, but they also forage in groups, depending on the size of the prey (Fowler & Gobbi 1988; de Carvalho 1998). This species inhabits a diversity of habitats that vary in resource levels and thus constitutes a good system to examine the interaction between hunger stress and prey size on the occurrence of group foraging. Previous to this study, *P. bistriata*'s populations have been studied in the Cerrado habitat of Brazil, a tropical savanna–dry forest (Fowler & Diehl 1978; Gobbi et al. 1979; Sandoval 1987; Fowler & Gobbi 1988; de Carvalho 1998). Although these studies report the existence of facultative group-foraging behaviour in *P. bistriata*, no population comparison was made to examine the interaction between hunger level and prey size.

This univoltine spider is typically found in dry forests, but it also frequents a diverse range of habitats from semiarid scrub to wet forests in southeastern South America (Levi 1992). The development of these spiders is completed after the seventh moult (Sandoval 1987) and its phenology can vary depending on the habitat type (Fernández Campón 2005). In the wet sites of this study area, adults are found in the austral summer, at the end of December and January, and in the dry sites, adults are found in early autumn, between March and April.

The *P. bistriata* colony is composed of a communal retreat and thread framework built by siblings. The framelines forming this framework radiate from the retreat. The individual capture webs built on this framework form sheets of webs in a vertical position. When participating in group foraging, individuals can move across several webs to arrive at the web where the prey landed. There can be several planar sheets radiating from a retreat or from a nearby tree. This arrangement of webs differs from those of *Metepeira* species because web sheets are built in two dimensions and do not contain core and peripheral webs as is the case in *Metepeira* (Uetz & Hieber 1997; Rayor & Uetz 2000).