New Zealand Journal of Zoology, 2008, Vol. 35: 237–242 237
0301–4223/08/3503–0237

Observations of *Portia africana*, an araneophagic jumping spider, living together and sharing prey

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Abstract Instances are documented of finding individuals of *Portia africana* in the field living aggregated in the webs of other spiders, in the nest complexes of other salticids, around solitary nests of other salticids, and around the nests of oecobiid spiders. Aggregation members included all active juvenile stages of *P. africana*, as well as adult males and females. More than one individual of *P. africana* sometimes fed on the same prey. Small juveniles of *P. africana* were more often than other stages found aggregated and more often observed feeding together. Small juveniles of *P. africana* surrounded the nests occupied by other salticid genera and nests occupied by oecobiid spiders. When the resident salticid or oecobiid attempted to leave or enter the nest, one of the *P. africana* juveniles lunged and captured it, after which other *P. africana* individuals sometimes joined to feed.

Z07061; Online publication date 4 July 2008
Received 14 December 2007; accepted 6 April 2008

Keywords araneophagy; cooperation; Oecobiidae; prey sharing; Salticidae; sociality; spiders

INTRODUCTION

Jumping spiders (Salticidae) have unique, complex eyes and vision based on exceptional spatial acuity (Land 1969, 1974; Jackson & Blest 1982; Blest 1985). Most salticid species do not live in webs and are instead hunting spiders that feed primarily on insects captured by vision-guided stalking (Richman & Jackson 1992; Jackson & Pollard 1996). However, remarkable predatory versatility has evolved in the salticid genus *Portia* (Harland & Jackson 2004). Besides hunting cursorially, the species from this genus build prey-capture webs, invade the webs of other spiders, and practice aggressive mimicry and prey on other spiders (Jackson & Wilcox 1998), but here we consider something that has not been reported before, evidence that *Portia* is sometimes a social predator.

The term "web" is rarely given a strict definition, but the least ambiguous examples of webs are probably prey-capture devices considerably larger than the spiders that build them (Foelix 1996; Craig 2003). This type of web is normally held in place by silk lines connected to vegetation, rocks, the ground or other features of the environment and these webs are usually envisaged as stand-alone silk edifices (i.e., their support structures are not other webs). There are, however, numerous exceptions known as "web complexes" (i.e., instances in which the web's support structures include other webs). Web complexes can reach enormous size and accommodate tens of thousands of individual spiders, sometimes with most of the individual webs in the complex being connected exclusively to other webs (Jackson 1979). Whether stand-alone or part of a web complex, an individual web is usually envisaged as a single spider's home, but there are exceptions to this rule as well. For example, adult females often share webs temporarily with newly hatched juveniles (Norgaard 1956; Bessekon et al. 1992) or with one or more courting males (Robinson & Robinson 1980), and subadult females often share webs with adult males (Jackson 1986a). There are also examples of individuals belonging to different species living together in shared individual webs or in web complexes (Krafft 1970; Jackson 1986b; Whitehouse 1986).

Instead of building webs, cursorial spiders often build silk nests. Typical salticid nests are tightly woven tubular structures, not much larger than the resident, and function as moulting, mating and oviposition sites, and as shelters when the salticid is quiescent. Although most salticid nests, like most webs, may be stand-alone structures occupied by solitary individuals, salticid nests are sometimes joined together in nest complexes, including nest complexes occupied by more than one salticid species (Jackson 1986c).

Web complexes and nest complexes are both common in habitats along the shore of Lake Victoria in East Africa (Jackson 1999). More recently, we observed groups of *P. africana* in these same habitats occupying the web and nest complexes of the other spiders. Here, as baseline natural-history information underlying current experimental studies, we summarise opportunistic observations from the field and also present findings from some more structured laboratory observations.

Particular attention was given to *Oecobius amboseli* (Oecobiidae), as this small spider species (adult body length, 1–2 mm) appeared to be especially important prey for *P. africana* juveniles. Found on tree-trunks, stones and the walls of buildings in Mbita Point and Entebbe, *O. amboseli*'s nests, like the nests of other oecobiids (Shear & Benoit 1974), is a small silk sheet (diameter, 30 mm or less) used as a shelter and as a device for detecting prey. *O. amboseli* tends to aggregate by placing its nests close together, but not with silk touching (i.e., not in nest complexes). We were especially interested in how *P. africana* captured this prey species.

MATERIALS AND METHODS

Our field sites were in Kenya (Mbita Point; the Thomas Odhiambo Campus of the International Centre for Insect Physiology and Ecology; 0°25′S, 34°12′E; altitude, 1148 m) and Uganda (Entebbe Botanical Gardens; 0°04′N, 32°29′E; altitude, 1182 m). Opportunistic observations were made when *P. africana* was found at various times during the day, with each observation period lasting 20–120 min.

Laboratory cultures were established from individuals of *P. africana* collected at both field sites, with standard spider-laboratory rearing and maintenance procedures being adopted (photo-period, 12L:12D; temperature, 25°C; relative humidity, 80%; for more details, see Jackson & Hallas 1986). *P. africana* individuals from these cultures were maintained for about 2 months in groups ("colonies") of 5–20. Each colony was in a large cage (1 × 1 × 1.5 m) made from wood and glass. Pieces of wood, arranged horizontally and diagonally in the cage, served as web-connection points and as multi-level platforms on which *P. africana* and other spiders rested and moved about.

Four colony types were established ($N = 9$ colonies for each type): (1) related spiderlings (siblings from the same eggsac, 20 individuals per colony, no adults present), (2) unrelated spiderlings (spiderlings that had different parents, 20 individuals per colony, no adults present), (3) unrelated adults (no spiderlings present, five individuals per colony) and (4) an adult female accompanied by 10–20 of her own progeny.

Web-building spiders (juveniles of *Nephilengys* sp. (body length, 12 mm) and cursorial spiders (*O. amboseli* and a salticid species, *Pseudicius* sp.) from *P. africana*'s habitat) were introduced to the cages and allowed up to 3 days to establish webbing within the cage before introducing *P. africana*. After introducing *P. africana*, vinegar flies (*Drosophila melanogaster*), house flies (*Musca domestica*), mosquitoes (*Anopheles gambiae*) and midges (*Chaoborus* spp. (Chaoboridae) and *Nilodorum brevibucca* Chironomidae)) were added *ad libitum*. From time to time, we also added juveniles of web-building spiders (*Nephilengys* sp. and *Tetragnatha* spp.) (all small juveniles, 2–3 mm in body length) and both adults and juveniles of *Argyrodes* spp. (Theridiidae) (all 2–3 mm in body length). *Argyrodes* is a genus of small spiders well known for living in the webs of spiders belonging to other genera (Foelix 1995). In East Africa, various species of *Argyrodes* also build their own webs isolated from the webs of other spider genera. The vinegar flies, house flies and mosquitoes, as well as some of the *Argyrodes*, were from laboratory cultures. The other arthropods were collected locally as needed.

Spiders were classed into three size groups: "small juveniles" (body length 1–3 mm), "large juveniles" (>3 mm) and adults (>8 mm). "Large individual" is a collective term for adults and large juveniles.

RESULTS

Aggregations of *Portia africana* observed in the field

In Mbita Point, there were four especially large web complexes (referred to as the "primary web complexes"), each occupied primarily by species from the genera *Argyrodes*, *Cyrtophora*, *Nephilengys* and *Tetragnatha*. Whenever observed, each primary web complex had at least one adult female of *P. africana* present, with one or more adult males and one or more juveniles (any instar) also present. Counting especially small juveniles tended to be difficult, but a total of 10 or more adult and large juvenile individuals of *P. africana* per primary web were typical. Groups of 2–5 large individuals of *P. africana*, sometimes accompanied by as many as 40 small juveniles, were also seen in smaller web complexes and in large solitary webs.

Small juveniles of *P. africana* were found in salticid nest complexes, with the primary salticid residents being *Menemerus* spp. and *Pseudicius* spp. A few adults and large juveniles of *P. africana* were seen in nest complexes but, in each of these instances, the nest complex was surrounded by a web or web complex. *P. africana*'s own webs were thoroughly integrated into the host webs, making it virtually impossible in most instances to determine whether *P. africana* was at any given moment on its own silk or the other spiders' silk (see Jackson & Blest 1982).

Observations of communal feeding in the field and in the laboratory

There were 14 observations of prey sharing by *P. africana* in the field (Table 1) and 25 in the laboratory (Table 2) (total number of observations of prey sharing, 39). In each instance, the prey was a spider.

Table 1 Observations of individuals of *Portia africana* feeding together on same prey in field.

Group composition	Prey	No. observed
Two adult females	*Nephilengys* sp. (Nephilidae)	1
One adult female and one adult male	*Nephilengys* sp. (Nephilidae)	1
One adult female and one large juvenile	Unidentified pholcid spider	1
One adult female and one small juvenile	*Nephilengys* sp. (Nephilidae)	1
One adult female and one small juvenile	*Tetragnatha* sp. (Nephilidae)	1
One adult female and two small juveniles	*Nephilengys* sp. (Nephilidae)	1
Two large juveniles	Unidentified araneid spider	2
Large juvenile + small juvenile	*Cyrtophora* sp. (Araneidae)	1
Two small juveniles	*Oecobius amboseli* (Oecobiidae)	2
	Menemerus sp. (Salticidae)	1
	Pseudicius sp. (Salticidae)	1
Three small juveniles	*Oecobius amboseli* (Oecobiidae)	1

Table 2 Observations of individuals of *Portia africana* feeding together on same prey in laboratory. Gp 1, related spiderlings; Gp 2, unrelated spiderlings; Gp 3, unrelated adults; Gp 4, adult female accompanied by her own progeny.

Group composition	Prey	No. observed	Group
Two adult females	*Nephilengys* sp. (Nephilidae)	1	Gp 3
Two adult females	*Portia africana* adult female (cannibalism)	1	Gp 3
One adult female and one large juvenile	*Nephilengys* sp. (Nephilidae)	1	Gp 4
Two large juveniles	*Nephilengys* sp. (Nephilidae)	1	Gp 2
Two large juveniles	*Tetragnatha* sp. (Tetragnathidae)	1	Gp 2
Two small juveniles	*Argyrodes* sp. (Theridiidae)	1	Gp 1
	Oecobius amboseli (Oecobiidae)	15	Gp 1, 4; Gp 2, 7; Gp 4, 4
	Pseudicius sp. (Salticidae)	1	Gp 2
Three small juveniles	*Oecobius amboseli* (Oecobiidae)	2	Gp 1, 1; Gp 2, 1
Four small juveniles	*Oecobius amboseli* (Oecobiidae)	1	Gp 4

There was one instance of four small juveniles feeding together on *O. amboseli* and six instances of three small juveniles feeding on one *O. amboseli*. There was one instance of two juveniles feeding alongside an adult female on *Nephilengys* sp. In all other instances, there were only two individuals feeding together. For small juveniles, the most commonly shared prey was *O. amboseli*. There were no instances of *P. africana* feeding together on insects. Sharing of prey in the laboratory was about equally often seen regardless of whether the spiderlings were related (Table 2).

Initiation of communal feeding

Small *P. africana* spiderlings readily clustered around the nests of *Oecobius* and salticids, and then remained quiescent. Occasionally, one of the *P. africana* spiderlings used its legs or palps to probe the silk of the nest. When the resident spider eventually came out of the nest, the nearest *P. africana* lunged and often captured it. If this attempt failed, the oecobiid or salticid ran away and the *P. africana* spiderlings usually remained at the nest. When the oecobiid or salticid returned later, it sometimes got caught by one of the waiting *P. africana.*

We did not observe the formation of feeding groups consisting of more than two individuals of *P. africana*, but we observed the formation of eight feeding pairs (6, the prey was an oecobiid; 2, a salticid). In each instance, the prey and both of the *P. africana* juveniles were about equal in body length. Prey sharing came about by one juvenile (the interloper) orienting and moving slowly towards the other juvenile, which was already feeding. The interloper usually moved around so as to approach the prey from the side opposite to the side from which the other individual was feeding. The feeding individual sometimes stepped away, carrying the prey away as it did so, but eventually the interloper moved in close and grabbed hold of the prey. When this happened, the joined individual sometimes dropped the prey item and stepped rapidly towards the interloper, with the interloper's response being to flee, only to return later. Once the two juveniles were feeding together on the same prey, one individual sometimes reached across and used its legs to slap at the other individual, and sometimes there were pulling matches between the two spiders. However, the two spiders usually soon settled down and quietly fed together. When the prey was in body length smaller than the *P. africana* juveniles, an interloper sometimes made repeated approaches, but the feeding individual kept moving away, carrying the prey along. In these instances, the interloper eventually gave up.

DISCUSSION

In the spider literature, the term "social" is commonly used when spiders of the same species live together and share prey (see Buskirk 1981; Aviles 1997) and calling *P. africana* "social" is consistent with this tradition. However, "sociality" and "social" can be problematic, as they are probably best accepted as terms for which insisting on strict definitions is ill-advised. Widely used technical terms, such as eusocial and subsocial, have usefully strict definitions, but we need to retain the broader term "social" for more casual usage (see Wilson 1975).

Seeing that *P. africana* lives in groups and shares prey, perhaps a more interesting question is whether this predator is cooperative, although the wisdom of attempting strict definitions of "cooperation" is also debatable. However, the basic implication of this word is that individuals in a group achieve a common goal by acting together, with no assumptions being made about the individuals being motivated by anything like awareness of a goal being shared. Our observations of prey capture and subsequent communal feeding by *P. africana* during encounters with *O. amboseli* appear to be "cooperative" in this basic sense of the word, but it is important to point out what is not meant by adopting this word here.

By using the term "cooperative", we do not automatically mean anything like being "altruistic". Nor does using this term imply that prey sharing was necessarily a peaceful concordance. When we observed the preliminaries to prey sharing, the behaviour of the individual with the prey appeared to be attempts to deny the intruder access to the prey (i.e., the individual with the prey routinely moved away, carrying the prey with it, or else appeared to be trying to drive the intruder away). Prey sharing, when it occurred, seemed to be something like the spiders reluctantly adopting a truce. A similar conclusion was suggested by the findings in a study of prey sharing by *Argyrodes flavipes*, a web-building Australian species from this genus that normally lives in aggregations of conspecific individuals (Whitehouse & Jackson 1998).

Whether or not the term "cooperation" is applicable to *P. africana* is, at this stage, a distracting secondary issue. We need to start by discerning the details of this predator's behaviour and then let these details frame the questions for further research that will be aimed at clarifying how this surprising discovery about *P. africana* relates to broader issues related to animal sociality and cooperation (see Whitehouse & Lubin 2005).

ACKNOWLEDGMENTS

We are especially grateful to Hans Herren, Christian Borgemeister, Bart Knols and Charles Mwendia at the International Centre for Insect Physiology and Ecology for the numerous ways in which they supported the research. Godfrey Otieno Sune, Stephen Alluoch, Silas Ouko Orima and Jane Atieno Obonyo provided invaluable technical assistance. We gratefully acknowledge support from the National Geographic Society (RRJ), the Royal Society of New Zealand (Marsden Fund; RRJ, SDP; James Cook Fellowship, RRJ). For taxonomic assistance, we thank Wanda Wesolowska, G. B. Edwards and Arthur Harrison.

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