**Original papers**

**Relationship between prey consumption and colony size in an orb spider**

David A. Spiller

Department of Zoology, University of California, Davis, CA 95616, USA

Received November 8, 1991 / Accepted in revised form February 7, 1992

**Summary.** I studied the relationship between prey consumption and colony size in the orb spider *Philoponella semiplumosa*. Observations of unmanipulated colonies showed that prey biomass per juvenile spider was positively correlated with colony size, indicating that prey consumption was highest in the largest colonies observed. In contrast, the relationship between prey biomass per adult female and colony size was curvilinear; prey consumption tended to be highest in intermediate-sized colonies. Adult female cephalothorax width was positively correlated with colony size. Number of egg sacs per adult female tended to be highest in intermediate-sized colonies. Prey biomass per juvenile was lower in experimentally reduced colonies than in large control colonies. Aerial-arthropod abundance was not correlated with colony size, and experimental prey supplementation did not affect colony size. Thus, the relationship between prey consumption and colony size was influenced by coloniality directly, rather than by a correlation between prey abundance at a site and colony size.

**Key words:** Spiders – *Philoponella* – Coloniality – Prey consumption – Competition

Possible advantages of group foraging have received much attention (review in Pulliam and Caraco 1984). In general, feeding rate may be higher for predators in groups than for solitary predators either because groups forage in areas with higher prey abundance or because interactions among group members enhance prey-capture success. Possible costs of grouping that can reduce feeding rate are interference and exploitative competition. Because these costs are expected to increase with group size, in large groups the costs may outweigh the benefits. Certain cost-benefit models show that maximum per capita feeding rate occurs in intermediate-sized groups (Wilson 1975; Brown 1982; Clark and Mangel 1984; Pulliam and Caraco 1984). This prediction is supported by field studies of large carnivores (Caraco and Wolf 1975; Nudds 1978; but see Packer et al. 1990). The relationship between foraging and group size may be further complicated by differences between dominants and subordinates (Brown 1982; Pulliam and Caraco 1984); in theory, when costs due to competition fall disproportionately upon subordinates, colony size in which feeding rate is maximum is smaller for subordinates than for dominants.

Social orb spiders (Araneidae, Uloboridae) live in colonies consisting of separate orbs that are interconnected by support lines or a communal barrier web. Typically, each orb is occupied by one spider and prey capture is not cooperative (reviews in Buskirk 1981 and Uetz 1986). However, other mechanisms may cause feeding rate to be higher for colonial than for solitary individuals. First, colonies may inhabit areas with higher prey abundance. Because colonies span large distances they can exploit certain sites that yield high food abundances – for example, gaps in forests (Lubin 1974, 1980; Rypstra 1979), across streams (Buskirk 1975a) and large cacti (Uetz and Burgess 1979). Second, foraging efficiency may be enhanced via the “ricochet effect” (Uetz 1989); prey are often captured in one orb after hitting another orb or several in succession. Uetz’s (1989) observations of *Metepeira* provide compelling evidence that this mechanism increases prey-capture success, particularly for large prey. In large colonies, however, the costs of competition may outweigh the benefits. Within large *M. incrassata* colonies prey-capture rate was higher for individuals on the periphery than for those near the center (Rayor and Uetz 1990). In addition, Lubin (1974) found that flying insects often avoided large *Cyrtophora moluccensis* colonies.

Thus, prey abundance, feeding rate and colony size may interact in various ways. Smith’s (1982, 1983) studies of semisocial *Philoponella oweni* showed that insect abundance, per capita feeding rate and fecundity were higher for colonies than for solitary individuals. Experimentally reduced colonies had higher feeding rates than control colonies, indicating that individuals within colo-
juveniles and adult females were computed separately to
Methods
juveniles (2-3 mm), adult females and adult males. Adult males
nial individuals varied among habitats in Costa Rica.
irregular barrier web and sits in the orb hub. Colonial individuals'
northern South America and throughout the Caribbean region
Philoponella semiplumosa
where prey are more abundant or 2) coloniality per se
consumption and colony size in the orb spider
high insect abundance outweighed the cost of com-
strate. Most colonies were approximately spherical but some were
above the ground, attached to low vegetation and limestone sub-
Eberhard (1979) found that relative numbers of solitary and colo-
Uloboridae). A positive relationship could be caused by: 1) larger colonies occurring
where prey are more abundant or 2) coloniality per se
encompassing foraging efficiency. To test the first hypothesis
I measured the relationship between aerial-arthropod
abundance and colony size; in addition, I experimentally
supplemented colonies with prey to observe the effect on
colony size. To test the second hypothesis I conducted a
eggs and estimated the body length (to the nearest mm)
of each prey item being consumed. Because it rained nearly every
ammonite from about 1000 to 1300 hr each day. I could
not distinguish individuals during the study, particularly in large
colonies, because they were not marked and they often changed
positions. I could not identify prey taxa because
Philoponella semiplumosa
wrap their prey in large amounts of silk; also, body lengths of some
prey may have been underestimated due to wrapping. Data on prey
consumption by adult males and hatchlings are not presented.
Adult males were observed feeding in only 7 colonies; in 4 of these
colonies only 1 observation of an adult male feeding was recorded.
Hatchlings were difficult to observe, especially when they were in
the center of large colonies; I observed them feeding less frequently
than juveniles and adult females but this may be biased. On 23 June
1985 I collected all adult-sized females and egg sacs at each site. In
the laboratory I counted the eggs in each sac, ascertained spider
maturity by inspecting the epigynum and measured cephalothorax
width of adults with an ocular micrometer.
To measure the relationship between aerial-arthropod abun-
dance and colony size, on 24 June 1985 I put a sticky trap at each
site that had been occupied by P. semiplumosa on the previous day (3 of the 18 unmanipulated sites had none). In addi-
tion, I put a trap at 5 vacant sites that were "similar" to occupied
sites during the trapping sessions. Although the vast majority of ar-
thropods caught by both orb spiders and aerial sticky traps are adult
insects, sticky traps may yield only a crude measure of prey avail-
ability because frequencies of certain taxa caught in traps and in
spider webs differ (Uetz and Biere 1980; Castillo and Eberhard 1983).

Observations of colony structure and persistence
On 17 April 1984 I put numbered tags next to the sites of all solitary
and colonial P. semiplumosa webs encountered until 20 sites were
tagged within an approximately 500 m² area. For each spider
I recorded the size/sex class and used a ruler to measure the distance
to the nearest neighbor with an orb. On 27 April 1985 I counted the
number of P. semiplumosa at each tagged site. On 27 April 1991
I measured the distance from the approximate colony center of each
spider within 6 colonies.

Observations of prey consumption and aerial-arthropod
abundance
On 29 May 1985 I put numbered tags next to the sites of all solitary
and colonial P. semiplumosa webs within an approximately 900 m²
area. Total number of sites tagged was 28; 10 were assigned to
manipulations (see below). From 29 May to 23 June 1985 I censused
each site daily. I counted the numbers of spiders in each size/sex
class and egg sacs and estimated the body length (to the nearest mm)
of each prey item being consumed. Because it rained nearly every
afternoon I censused from about 1000 to 1300 hr each day. I could
don not distinguish individuals during the study, particularly in large
colonies, because they were not marked and they often changed
positions. I could not identify prey taxa because
Philoponella semiplumosa
colony size, suggesting that in large colonies the costs of
competition outweighed possible foraging benefits
(Riechert et al. 1986; Ward and Enders 1985; Seibt and
Wickler 1988).
In this study I measured the relationship between prey
consumption and colony size in the orb spider
Philoponella semiplumosa (Uloboridae). A positive rela-
tionship could be caused by: 1) larger colonies occurring
where prey are more abundant or 2) coloniality per se
enhancing foraging efficiency. To test the first hypothesis
I measured the relationship between aerial-arthropod
abundance and colony size; in addition, I experimentally
supplemented colonies with prey to observe the effect on
colony size. To test the second hypothesis I conducted a
egy, and measured cephalothorax
width of adults with an ocular micrometer.
Spider classes and colony size
I divided the spiders into 4 size/sex classes: hatchlings (≤1 mm),
juveniles (2-3 mm), adult females and adult males. Adult males
were easily distinguished by their dark, swollen pedipalps. In the
field it was difficult to ascertain whether a female was mature;
I assumed that individuals ≥ 4 mm were adults. Most juveniles and
adult females had orbs, and I observed both classes building orbs
and adding silk to the communal web. I never observed an adult
male building an orb or adding to the communal web. Hatchlings
had no web or tiny ones, and they probably contributed very little
to the communal web. Therefore, to quantify colony size I used the
number of juveniles and adult females combined. I did not use total
number of individuals because it would have yielded some deceptive
 colony sizes; for example, a single female with a brood of hatchlings
would have a larger value than colonies with several juveniles and
adult females.

Methods

Study species and site
Philoponella semiplumosa is distributed from southern Texas to
northern South America and throughout the Caribbean region
(Opell 1979). The spider builds a horizontal orb attached to an
irregular barrier web and sits in the orb hub. Colonial individuals’
webs are interconnected by a common barrier web. Lahmann and
Eberhard (1979) found that relative numbers of solitary and colo-
nial individuals varied among habitats in Costa Rica.
I studied P. semiplumosa in a forested area on Iron Cay, a small
island off Great Abaco, Bahamas. Their webs were about 0.1–0.5 m
above the ground, attached to low vegetation and limestone sub-
strate. Most colonies were approximately spherical but some were
quite irregular. Adult females were 4–6 mm in body length; adult
males were 3–4 mm. Adult females attached their egg sacs to the
barrier close to their orbs. When hatchlings emerged they were
slightly less than 1 mm. They aggregated around the egg sac for
about 3–7 days and dispersed gradually. Their first webs were very
small and sheet-like, as in other uloborids (Eberhard 1977; Opell
1979).

Spider classes and colony size
I divided the spiders into 4 size/sex classes: hatchlings (≤1 mm),
juveniles (2-3 mm), adult females and adult males. Adult males
were easily distinguished by their dark, swollen pedipalps. In the
field it was difficult to ascertain whether a female was mature;
I assumed that individuals ≥ 4 mm were adults. Most juveniles and
adult females had orbs, and I observed both classes building orbs
and adding silk to the communal web. I never observed an adult
male building an orb or adding to the communal web. Hatchlings
had no web or tiny ones, and they probably contributed very little
to the communal web. Therefore, to quantify colony size I used the