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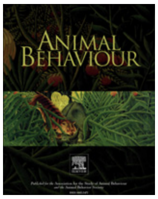

Settling where the food is: prey abundance promotes colony formation and increases group size in a web-building spider

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The parasocial-route hypothesis postulates that coloniality in spiders is driven by the occurrence of high prey densities. This hypothesis is partially supported by comparative studies of colonial species. However, experimental evidence is lacking to confirm that prey availability directly promotes colony formation. We used the web-building spider *Cyrtophora citricola* (Araneidae) as a model species to investigate the effect of prey availability on coloniality. We conducted field surveys on colonies located on acacia trees in the Arava valley, Israel, to compare colony group size between sites differing markedly in insect abundance. We then performed experiments in net houses to test (1) the effect of prey remains in the females' webs on juvenile establishment decisions and (2) the effect of food supply on web site fidelity of juveniles. Colony group size and reproductive investment were greater in prey-rich sites than in poor sites. In the experiments, juveniles released on adult females' webs that contained remains of prey consumed by the adults were more likely to settle than those released on empty webs. Once established, food deprivation slightly increased the number of juveniles leaving the female's web, suggesting that they are reluctant to disperse after settlement. Relocation in *C. citricola* is costly, as their webs demand high energy investment. Hence, cues of prey availability are crucial, enabling spiders to acquire information about habitat quality before investing in web construction. Together, our findings provide evidence that prey availability facilitates coloniality and thus supports the parasocial route in the evolution of spider group living.

Habitat selection is a trait with strong implications for individual fitness, and a wide variety of strategies used by animals to select a suitable environment have been described (Morris 2003). Among the factors that play a role in site selection are predation risk (Díaz et al. 2006; Thomson et al. 2006), microclimate conditions (Wilson 1998; Kolbe & Janzen 2002) and abundance of food resources (Stapp 1997; Walther & Gosler 2001). Cues available to an organism in the environment can give information about habitat suitability and quality. In addition, animals that live in groups either permanently or during part of their life cycle can cue in on features of their conspecifics that provide information about the habitat (Aragon et al. 2006; Salomon 2009). For example, group members may provide cues regarding food availability or quality (Boulinier et al. 2008).

Among more than 41 000 described species of spiders (Platnick 2010), approximately 60 are known to live in groups. Group-living spiders are classified into three categories: social, subsocial and colonial. Most subsocial and social spiders are web-building species that live in communal webs, and individuals cooperate in prey capture and care of the young to different degrees. Colonial spiders, by contrast, occur in aggregations of individual webs in which spiders catch their own prey and breed independently (reviewed in Whitehouse & Lubin 2005; Lubin 2010). In some colonial species, spiders can decide either to build a solitary web or to build a web within the framework of a colony. Coloniality in spiders is thus facultative and much effort has been invested in discovering the local factors that promote it (Uetz & Hieber 1997). Among the advantages of coloniality versus living solitarily are increased prey capture, greater web-building efficiency by reducing silk costs and protection against predators and parasites (Uetz 1989; Lloyd & Elgar 1997; Uetz et al. 2002). However, living in colonies imposes costs, namely risk of cannibalism, competition for prey, disease or parasite transmission and even increased visibility to predators (Elgar 1989; Hieber & Uetz 1990; Leborgne et al. 1998).

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According to optimal-foraging models (Charnov 1976; Krebs & Davies 1997), animals adjust their foraging behaviour to maximize their energy intake, thereby selecting the habitats with highest expected returns. At the same time, individuals have to balance the potential costs of searching for foraging sites, such as predation risk and competition (Nonacs 2001). Assessing prey availability in a site before settling is critical to web-building spiders because construction of a web requires investment of energy and relocation is both expensive and risky (Tanaka 1989; Zschokke & Vollrath 2000). Solitary web-builders have two ways of retrieving information about this key feature of habitat quality. The first plays a role in site selection and concerns habitat assessment before settling using indirect cues of prey presence (Pasquet et al. 1994; Herberstein et al. 2000). The second, influencing fidelity to a web site, takes place after settling and involves assessment of prey capture and habitat stability (McNett & Rypstra 1997; Nakata & Ushimaru 1999).

Studies on colonial spiders show that prey availability is positively correlated with colony group size (Uetz et al. 1982; Smith 1985) and with increased tolerance towards other individuals (Hodge & Uetz 1995). Even solitary web-building spiders sometimes occur in temporary aggregations at sites with high insect density (Rypstra 1985). If living in colonies located in prey-rich areas results in a higher fitness to individuals, the behaviours leading to settling and remaining in such colonies should be favourably selected, potentially leading to the evolution and maintenance of coloniality (Uetz et al. 1982). Therefore, it is thought that coloniality in spiders is driven by the occurrence of high prey densities at certain sites, an evolutionary pathway to group living that is referred to as the 'parasocial route' (Michener 1969; Shear 1970; Whitehouse & Lubin 2005). Nevertheless, there is no experimental evidence that food availability directly promotes colony formation and the mechanisms connecting food availability at a site to group size and individual fitness remain largely unexplored.

In this study, we used the colonial web-building spider *Cyrtophora citricola* (Araneidae) to investigate the relationships between prey availability, colony group size and female reproductive success, and the role of prey cues and availability in determining juvenile web site selection. *Cyrtophora citricola* occurs in the Mediterranean basin, subtropical and tropical areas of Asia, Africa and Australia (Blanke 1972), and has recently colonized the American continent (Alvares & De Maria 2004). It adapts to a wide range of habitats, from mesic areas to deserts and anthropogenic ecosystems such as gardens and citrus groves (Leborgne et al. 1998; Piñol et al. 2010). The web of *C. citricola* is a three-dimensional structure composed of a nonsticky horizontal orb web with an open hub and a tangle of threads above and below the orb web. Within a colony, the individual web is a territory and the owner responds aggressively towards invaders, although spiders tolerate meeting one another in the communal network (Lubin 1974). Females produce up to 10 cocoons arranged in a string where every new cocoon is placed below the previous one. They do not show maternal care but tolerate spiderlings in their web. Juveniles may remain in the parent colony and construct small webs within the tangle of threads of the adult webs, or disperse to join another colony or to establish a new one (Blanke 1972; Y. Lubin, personal observations). Individuals of *C. citricola* are facultatively colonial and have flexible behaviour with regard to decisions of joining or leaving a colony (Whitehouse & Lubin 2005). Thus, *C. citricola* appears to be an excellent model species to investigate the relationship between web site selection and prey availability.

We adopted the parasocial-route hypothesis as a conceptual framework to predict that local prey enhancement enables *C. citricola* colonies to increase in group size, and propose higher reproductive success and immigration of juveniles as possible mechanisms by which prey availability could favour coloniality. To test our predictions we addressed three main questions. (1) Do colonies in sites with high insect abundance host more spiders and is the reproductive output of females higher? (2) Do indirect cues of food availability influence juvenile decisions to settle in a colony? (3) Does food supply affect site tenacity of established juveniles?

METHODS

Field Surveys

Colonies of *C. citricola* are found on scattered acacia trees (mainly *Acacia raddiana* and *A. tortilis*) in dry washes and oases near springs (Rao & Lubin 2010) in the Arava valley, a hyperarid region along the Afro-Syrian rift valley, southern Israel. Nineteen acacia trees with colonies were surveyed in spring (15–29 March) and early summer (27 May–1 June) of 2009. A group of trees ($N = 8$) was selected from two sites near an organic fertilizer depot (hereafter referred to as 'compost sites') that attracted large numbers of flies. The other group of acacia trees ($N = 11$) was surveyed at 'noncompost sites' along a gravel road at increasing distances from the two fertilizer depot sites. Among the trees occupied by *C. citricola* colonies at every site, we chose ones that allowed easy access and inspection of the spider webs. To ensure spatial independence, all selected trees within a site were separated by a minimum distance of 50 m, and the trees from noncompost sites were at least 2 km from the compost sites. Since in the surroundings of the focal trees and over the whole study area there were many other acacia trees, we considered it highly unlikely that spiders moved from one focal tree to another during the observation period.

In the first survey (March), tree canopy height and two perpendicular canopy diameters were measured to calculate tree canopy volume. All spiders from a single tree were considered to belong to the same colony, although webs tended to cluster together in groups of different sizes connected by frame threads. To estimate colony volume, we measured three dimensions of all the groups in the tree and summed the resulting volumes. For each group, we counted the juveniles, males, subadult and adult females, cocoon strings and cocoons. When a group was too large or not easily accessible in all its volume, a 50×50 cm frame was randomly placed in front of the webbing and all spiders, strings and cocoons within a prism defined by the frame and the depth of the webbing were counted. The prism population estimates were multiplied by the estimated number of prisms in the total web volume. All measurements were taken to the nearest centimetre with a retractable tape measure except canopy height, which was taken with the aid of a telescopic measuring stick. Females sitting below a cocoon string and females of similar size to these were considered to be adults. The number of males and juveniles was pooled in the analyses because of the difficulty of reliably distinguishing them in the field: the size and colour of an adult *C. citricola* male are the same as those of a juvenile and its swollen pedipalps are only visible in frontal view.

In the second survey (May) there were few spiders in the colonies and the empty webs looked old, and most were partially destroyed. Following the same methodology as in the first survey, we counted the strings and cocoons in each colony.

Flying insects were sampled on the periphery of each of the acacia trees used in the surveys. Two sticky traps (23×14 cm) were hung in each of the trees for a 24 h period at the end of the first and second surveys. The traps were placed in the tree canopies at a height of 2 m next to the colonies, on the south and east side of the tree. After removal, the trapped insects on both sides of the