Anti-predator crèches and aggregations of ant-mimicking jumping spiders (Araneae: Salticidae)

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Myrmarachne assimilis, an ant-like jumping spider (Araneae, Salticidae) from the Philippines and a Batesian mimic of *Oecophylla smaragdina*, the Asian weaver ant, aggregates on leaves in the company of its model. All stages in this species' lifecycle are sometimes found in nest complexes (nests connected to each other by silk). Although aggregating and forming nest complexes is known for a few other salticid species, the aggregations of *M. assimilis* have some unusual characteristics. In particular, reproductive females appear to be most frequently found with other reproductive females in nest complexes, suggesting that nest complexes have a role in parental care and are often built by females joining other females. An egg-survival experiment showed that eggs in solitary nests were more often destroyed than were eggs in nest complexes, suggesting that, for females of *M. assimilis*, choosing aggregations as oviposition sites may be functionally akin to life insurance for their progeny.   © 2008 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2008, **94**, 475–481.

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INTRODUCTION

Although terms such as 'eusocial' and 'semisocial' have been given strict definitions in the insect literature, it is counterproductive to insist on formal definitions of the broader, everyday terms 'social' and 'sociality' that are routinely and casually used for species that tend to form groups of conspecific individuals (Wilson, 1975). Sociality in spiders is of exceptional interest because the popular impression is that these predatory arthropods are highly aggressive toward members of their own species and prone to cannibalism, and such behaviour that would not appear conducive to sociality. Among the more than 5000 species in the largest spider family, the Salticidae or jumping spiders, examples of sociality are

especially scarce. The better-known examples of sociality come instead from web building species belonging to other families (Avilés, 1997; Avilés *et al.*, 2001; Whitehouse & Lubin, 2005).

Having unique, complex eyes that support exceptional spatial acuity (Land, 1985; Land & Nilsson, 2002; Harland & Jackson, 2004), most salticids are solitary hunters that spend their lives outside webs (Richman & Jackson, 1992). Yet there are examples of salticids aggregating. Crane (1949) reported finding 14 individuals, including juveniles, adult males, and adult females, of *Semorina megachelyne* in Venezuela living together in a 'large silk shelter'. Numerous salticid species from temperate regions sometimes form over-wintering aggregations of tightly clustered individual nests under the bark of trees and under stones, with these aggregations being abandoned when winter quiescence ends (Kaston, 1948; Jennings, 1972). The largest aggregations of salticids are formed by approximately six salticid species that that live together in nests interconnected by silk

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('nest complexes') in habitats near the shore of Lake Victoria in Kenya and Uganda (Jackson, 1986a, b, 1999; Wesolowska & Salm, 2002; Wesolowska, 2006).

With one exception, the function of aggregating is poorly understood in salticids. The exception is a type of nest complex that appears to be almost universal in the Salticidae, with the formation of these complexes functioning as a male mating tactic known as 'cohabitation' (Jackson, 1986c; Jackson & Pollard, 1997). Adult males, upon encountering nests occupied by subadult (one instar short of maturity) females, typically respond by building adjoining nests of their own, waiting for subadult females to moult, and then mating inside the females' nests.

In the present study, we consider the function of aggregations formed by *Myrmarachne assimilis*, a Batesian-mimic salticid from the Philippines that lives on leaves and aggregates by building nests close together on the same leaf. Batesian mimics are palatable individuals that deceive potential predators by resembling unpalatable or dangerous models (Wickler, 1968; Edmunds, 1974, 1978; Vane-Wright, 1980; Ruxton, Sherratt & Speed, 2004). All species in the salticid genus *Myrmarachne* are antlike (myrmecomorphic) (Wanless, 1978; Jackson & Willey, 1994), with different species tending to match the appearance of different sympatric ant species (Cushing, 1997; Edmunds, 2006). Besides being especially abundant insects in most terrestrial habitats (Hölldobler & Wilson, 1990), ants are notorious for their defensive adaptations, which include powerful mandibles, poison-injecting stings, formic acid, and the ability as social insects to mount communal attacks (Eisner, 1970; Blum, 1981). Ants are also especially important predators of many of the arthropods that might prey on a salticid, including other salticids (James *et al.*, 1999; Nelson *et al.*, 2005). All *Myrmarachne* species appear to be Batesian mimics (Cutler, 1991; Nelson & Jackson, 2006; Nelson *et al.*, 2006).

Myrmarachne assimilis is an especially accurate Batesian mimic of a particular ant species, the Asian weaver ant, *Oecophylla smaragdina* (Nelson *et al.*, 2005). *Oecophylla smaragdina* colonies often dominate the arboreal habitats in which they are found (Vanderplank, 1960; Lokkers, 1986). As a Batesian mimic with a close resemblance to a particular model species, *M. assimilis* might, by living especially near to this particular model, increase its protection from predators that are averse to the model (Edmunds, 2000). However, soldiers of *O. smaragdina* defend the colony and the workers are aggressive predators (Hölldobler & Wilson, 1977, 1978, 1990; Hölldobler, 1983) that sometimes kill *M. assimilis* (Nelson *et al.*, 2004, 2005). Predatory assaults on their progeny (Jackson & Willey, 1994) may be an additional risk for the reproductive individuals of *M. assimilis* that take

up residence in the company of *O. smaragdina*. In the present study, we characterize the nest aggregations of *M. assimilis* and consider whether clustering nests might function to protect the progeny of *M. assimilis* from ants.

MATERIAL AND METHODS

SAMPLING

The study site comprised a mango orchard in Los Baños (Laguna Province, Luzon, the Philippines). By visual inspection, we sampled all leaves that were reachable without the use of a ladder (at dusk, one tree per evening), with a proviso that the same tree was never sampled more than once. Four nest types were recognized (Table 1).

Single nest: measured from closest side, at least 10 mm from nearest neighbouring nest.

Nest complex: two or more touching nests (i.e. nests that have contiguous silk; Jackson, 1986c) (each individual nest in a complex is referred to as a 'complex nest').

Nest cluster: two or more nests that are close (i.e. nearest sides no more than 2 mm apart), but with no nest touching another nest (each nest in a cluster is referred to as a 'cluster nest').

Nest combination: a nest within 2 mm of a nest complex, but not touching another nest (each nest that did not touch another nest is referred to as a 'combination nest', but each nest that did touch another nest is referred to a complex nest within the combination).

Group nest: collective term for complex, cluster or combination nest.

Table 1. Number of *Myrmarachne assimilis* from each category found in different nest types (see text for definitions) found in the field.

Nest type	N
Single	698
Two-nest complex	475
Three-nest complex	193
Two-nest cluster	95
Three-nest cluster	46
Four-nest cluster	13
Nest combination (two-nest complex + combination nest)	140
Total	1660

Nontouching nests for which nearest sides were 2–10 mm apart were rare and were ignored. With this rule, we could distinguish unambiguously between single and group nests.

The identities of all nest occupants were recorded, with seven categories being recognized: progeny [unhatched eggs in nest, postembryos (inactive post-hatching stage clustered in nest), and hatchlings (active individuals one stage beyond postembryo, clustered in nest)]; juvenile (larger than hatchlings but not yet subadult); subadult female (based on size, probably one instar short of sexual maturity); subadult male (as revealed by enlargement of palps, one instar short of sexual maturity); nonreproductive female (adult female without progeny); reproductive female (adult female with progeny); adult male.

Eggs, postembryos, hatchlings, and adult males were readily identified without collecting (males are easily identified because they have greatly elongated chelicerae). Each other nest occupant was taken into a glass vial. Using a cotton-wool plug, we immobilized the spider at the bottom of the vial and then inspected it with a hand-held magnifying glass, after which the spider was returned to the leaf on which it had been found.

Myrmarachne assimilis normally takes shelter in nests before dusk and the very few individuals observed outside nests when sampling were ignored. Single unoccupied nests and group nests for which no constituent nest was occupied, also being rare, were ignored.

Our particular interest was to ascertain the kinds of groupings found in the field. Accordingly, we took each individual found in a group nest and investigated whether there were other individuals in the same group nest and, if so, the identity of these other individuals. This resulted in our sample size not corresponding precisely to the number of individuals found when sampling (i.e. N is instead the number of each combination of the seven recognized categories that were found together). For example, when a nest complex was shared by two reproductive females, we recorded two instances of a reproductive female in a nest complex with another reproductive female, and when a nest complex was shared by a male, a subadult female and a juvenile, we recorded one instance each of a male with a subadult female, a male with a juvenile, a subadult female with a male, a subadult female with a juvenile, a juvenile with a male, and a juvenile with a subadult female.

Data were analysed using chi square tests of independence and of goodness of fit, with Bonferroni adjustments to alpha whenever the same data set was used for multiple comparisons.

EGG-SURVIVAL EXPERIMENT

Egg survival with and without the reproductive female present was recorded for single nests and for three-nest complexes. The experimental site was the same as the sampling site, but the trees used for the experiment were different from the trees used for sampling. We first located reproductive females that were with eggs in single nests and reproductive females that were with eggs in three-nest complexes with no other spiders present in these complexes (three-nest complexes were chosen because examples that met this criterion were relatively accessible). The females were then removed at dusk from experimental nests (25 single nests and 30 nest complexes) but left in control nests (33 single nests and 30 nest complexes). Spiders were removed by prodding the nest with a soft brush until the female left, not noticeably damaging the eggs or nest in the process. Over a period of 5 days, we checked the experimental and control nests at dawn, recording for control nests whether the female was present or absent, for experimental and control nests whether the eggs were present or absent, and for all nests whether there were any ants on or in the nest. Data were analysed using Fisher's exact tests.

RESULTS

DISTRIBUTION OF ADULT MALES AND SUBADULT FEMALES

Adult males were usually found in single nests (Fig. 1). However, when males were found in group nests, it was primarily in nest complexes (nests that have contiguous silk) and overwhelmingly in the presence of subadult females (i.e. cohabitation) (Fig. 2E). Most subadult females were cohabiting with males when found (Fig. 2C).

DISTRIBUTION OF SUBADULT MALES, JUVENILES AND UNATTENDED PROGENY

Subadult males and juveniles were distributed similarly to adult males but different from subadult females (usually found in single nests) (Fig. 1). Few subadult males were found in group nests of any kind ($N = 15$) and, when found in group nests, they were usually alone (Fig. 2D). Cluster nests (nests in close proximity but not contiguous) were typically formed by juveniles but, otherwise, there was no pronounced pattern in the distribution of subadult males and juveniles across the different types of group nests (Fig. 2D, F). Unattended progeny were found in single nests on three occasions, but were usually found in group nests, most often in complexes rather than in
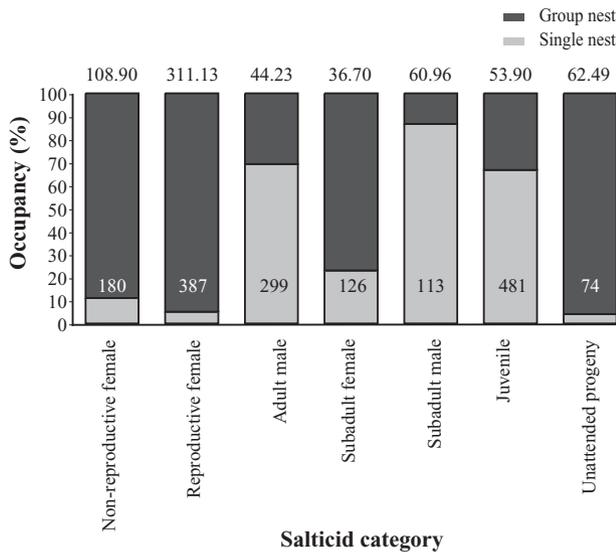
Figure 1. Percentages of each category of *Myrmarachne assimilis* found in single nests and in group nests. Because chi-square tests of goodness of fit revealed no significant differences between numbers of each spider category in two-nest complexes when compared with combined data from other group nests, these data were pooled and referred to as 'group nests'. Unattended progeny includes eggs, postembryos, and hatchlings. Sample sizes are shown within each bar. Chi-square values (tests of goodness of fit, null hypothesis 50/50 for occupancy of single versus group nest) are denoted above each bar. In each case, $P < 0.001$.

clusters (Fig. 2G), and they tended to be either with other unattended progeny or with nonreproductive females.

DISTRIBUTION OF REPRODUCTIVE AND NONREPRODUCTIVE FEMALES

Females, whether reproductive or nonreproductive, were most often in nest complexes. Reproductive females were found together, the only exception being that, in three-nest clusters, reproductive females were found alone (only a few reproductive females were in three-nest clusters) (Fig. 2B). Nonreproductive females were primarily, and approximately equally often, found with other nonreproductive females, reproductive females, and unattended progeny, except that it was rare that they were with unattended progeny in clusters (Fig. 2B).

OVERVIEW OF DISTRIBUTION PATTERNS

The majority of occupied nests in the field were group nests (Table 1), but adult males, subadult males, and juveniles were found more often in single nests than in group nests. This contrasted with females (reproductive and nonreproductive) and unattended

progeny which were present in group nests more often than in single nests (Fig. 1).

The distribution of most salticid categories within group nests was decidedly nonrandom, with clear differences between the distribution patterns of complexes and clusters. For simplicity, data from combination nests are not discussed, although the trends with these nests tend to correspond with the trends of nest complexes (Fig. 2). Out of the total number of spiders from each category found in groups nests, more nonreproductive females ($\chi^2 = 90.23$, $P < 0.001$), reproductive females ($\chi^2 = 276.73$, $P < 0.001$), males ($\chi^2 = 107.80$, $P < 0.001$), subadult females ($\chi^2 = 75.58$, $P < 0.001$), unattended progeny ($\chi^2 = 87.72$, $P < 0.001$), and juveniles ($\chi^2 = 7.89$, $P < 0.01$), but not subadult males ($\chi^2 = 0.56$, $P = 0.46$), were in nest complexes than in clusters.

Subadult females and reproductive females were in nest complexes at similar frequencies ($\chi^2 = 0.25$, $P = 0.616$), but subadult females were more often than subadult males in complexes ($\chi^2 = 10.11$, $P = 0.018$). When a male was in a complex nest, it was more likely to be an adult than a subadult male ($\chi^2 = 17.02$, $P < 0.001$).

Nonreproductive females were more likely to be found in nest complexes than were adult males ($\chi^2 = 5.80$, $P = 0.032$) but not reproductive females ($\chi^2 = 0.46$, $P = 0.499$), whereas reproductive females ($\chi^2 = 17.07$, $P < 0.001$) and unattended progeny ($\chi^2 = 15.31$, $P < 0.001$) were more likely to be present in complex nests than were juveniles.

EGG SURVIVAL

On eight occasions, ants (in each instance: *O. smaragdina*) were observed walking on single nests with females present, but only one of these nests was without eggs when next observed. However, when eggs were unattended, ants were seen walking on the nest on ten occasions (eight *O. smaragdina* and two unidentified ant species) and only two of these ten eggsacs (both with *O. smaragdina*) survived the 5-day observation period. There were four observations of *O. smaragdina* walking on the nests containing eggsacs in three-nest complexes with females present, and all of these eggsacs survived. There were six observations of ants walking on nests containing eggsacs in three-nest complexes from which females had been removed (five *O. smaragdina* and one unidentified ant species), but only one of these eggsacs failed to survive the observation period (ants: *O. smaragdina*).

Eggs in single nests were destroyed more often ($\chi^2 = 7.81$, $P = 0.019$) when the female was absent (ten of 25 destroyed) than when the female was present (three of 33 destroyed) (Fig. 3). However, in three-nest complexes, there was no difference in egg survival
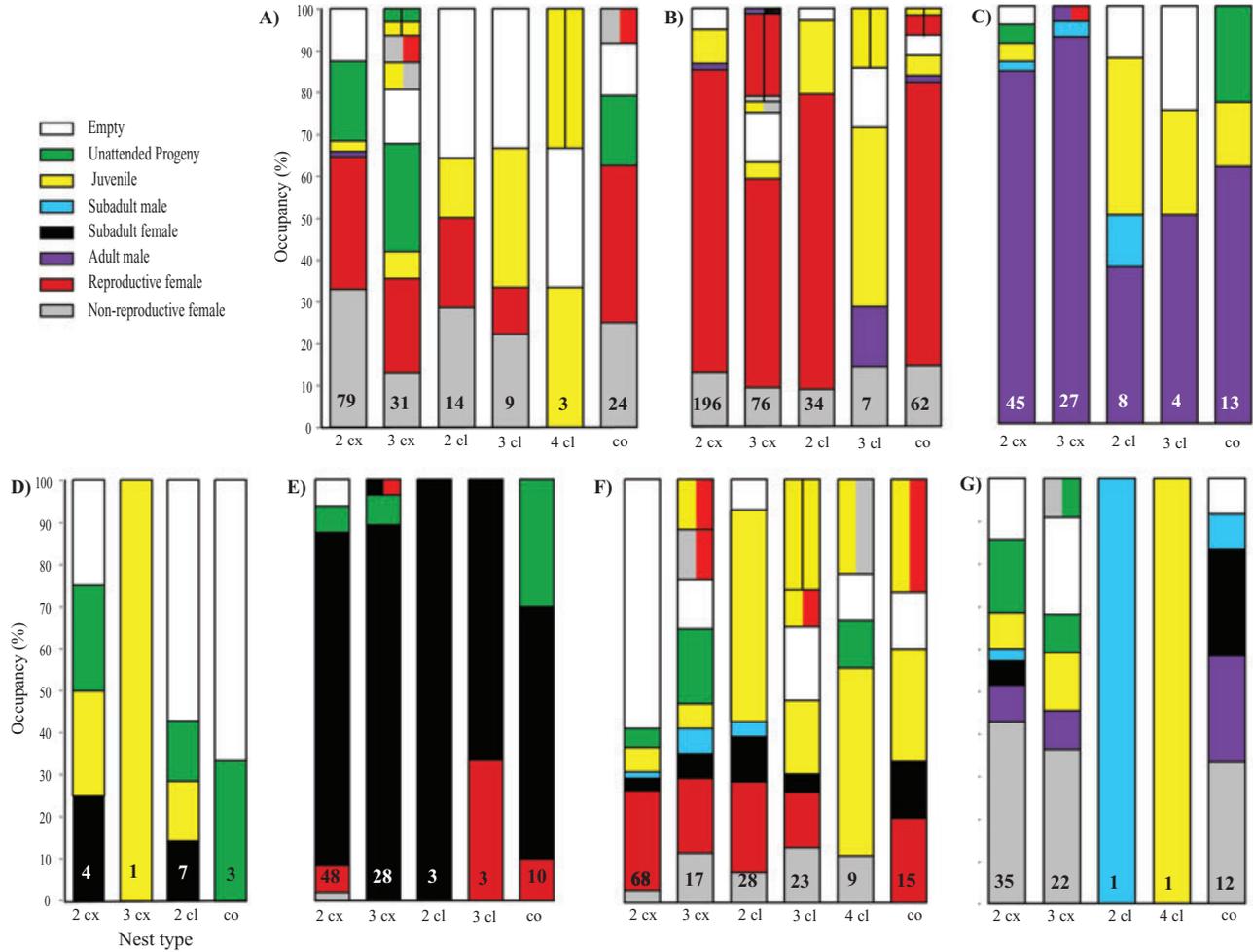
Figure 2. Distribution patterns of different categories of *Myrmarachne assimilis* associated with different nest types. A, nonreproductive female. B, reproductive female. C, subadult female. D, subadult male. E, adult male. F, juvenile. G, unattended progeny. Sample sizes are shown within each bar. Where two colours are shown, this indicates that one of each spider category is found in that nest type. A line down the middle depicts instances of two spiders of the same category being found in a particular nest category. cx, nest complex; cl, nest cluster; co, combination nest; a prefix number indicates the number of nests comprising each nest type. Where a nest type is missing from the histogram, the respective salticid category is not found within the indicated nest type. Unattended progeny comprise eggs, postembryos, and hatchlings.

depending on whether females were present or absent ($\chi^2 = 4.66$, $P = 0.237$). Furthermore, when females were absent, eggs in single nests were destroyed more often (ten of 25 destroyed) than eggs in three-nest complexes (three of 30 destroyed) ($\chi^2 = 6.80$, $P = 0.024$) (Fig. 3). Individuals of *M. assimilis* were never observed to attack ants or actively attempt to drive them away, but they often spun silk from inside the nest, suggesting that they were reinforcing the silk barrier between the ant and the nest interior.

DISCUSSION

Although aggregating and forming nest complexes is known for a few other salticid species, the aggregations

of *M. assimilis* are atypical because adult females appear to be the most frequent occupants of nest complexes, suggesting that the pattern is for nest complexes to originate when females join other females. Finding that egg survival was higher in group nests than in single nests suggests that aggregating has a role in parental care. For *M. assimilis* females, ovipositing in nest complexes appears to function as analogous to a life insurance for the progeny.

Perhaps the best-known example of aggregating by spiders that do not build webs occurs in Australian crab spiders (Thomisidae). These aggregations, however, are kin groups consisting of a mother and her offspring at various developmental stages (Evans, 1998) but our data provide little support for the
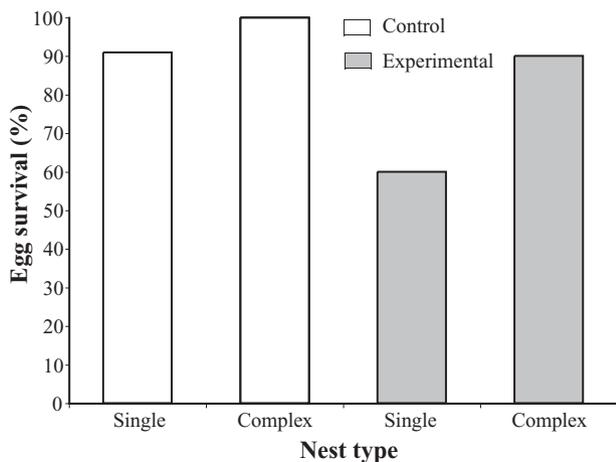
Figure 3. Egg survival in single nests and complex nests with females present (control) and absent (experimental).

notion that the aggregations of *M. assimilis* are based on kin groups. It was common to find progeny, whether attended or unattended, in nest complexes, whereas juveniles, subadult males, and adult males were found in single nests more often than in group nests. These findings suggest three hypotheses: (1) once past the hatchling stage, young spiders disperse from nest complexes and build solitary nests; (2) when males mature, they join subadult females (cohabitation); and (3) when females mature, they join each other to form nest complexes. That is, nest aggregating by *M. assimilis* appears to be driven by two primary factors, females joining other females and males joining subadult females. Cohabitation appears to function as a routine mating tactic for *M. assimilis*, much as it does for salticids in general (Jackson, 1986c; Jackson & Pollard, 1997), whereas females joining other females appears to function primarily as an anti-predator defence and especially as a method of defending progeny.

In the literature on social spiders, it has often been argued that enhanced foraging success is a principal adaptive advantage of aggregating (Nentwig, 1985; Rypstra & Tirey, 1991; Kim, Krafft & Choe, 2005; Whitehouse & Lubin, 2005) and that this advantage is especially applicable to kin-based groups, but we have no evidence that aggregating by *M. assimilis* is related to foraging, or that it involves kin groups. For this mimic, it appears that protection from predators, especially its own model, has been a primary selection pressure favouring aggregation, and, thus, protection from ants is especially relevant to progeny.

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