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# Maintenance of sociality in a communal caterpillar, *Eucheira socialis westwoodi* (Lepidoptera: Pieridae)

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## ABSTRACT

**Background:** The theory of kin selection fails to explain the maintenance of gregariousness in insects with low levels of relatedness. Alternative proposals suggest that other factors such as group thermodynamic efficiency or predator avoidance are greatly enhanced by insects living socially, and therefore might serve as reinforcements for costly social behaviours exhibited by these species independent of relatedness.

**Questions:** Do *Eucheira socialis westwoodi* (Lepidoptera: Pieridae) females place their egg masses near conspecific egg masses? Does the distance between egg masses influence the survival of the larvae hatched from these egg masses? Does group size influence larval foraging success?

**Organism:** *Eucheira socialis westwoodi* larvae from naturally occurring colonies in El Madroño, Durango, Mexico.

**Methods:** We assessed the distribution of egg masses on trees and across trees. Larvae from egg masses oviposited at variable distances from conspecific egg masses were followed until the fourth instar. Differently sized larval groups were constructed and maintained on 'artificial trees' using sprigs collected from a single host tree (*Arbutus xalapensis*: Ericaceae). These were in turn deployed to a semi-natural area. Frequency and duration of foraging of individually marked larvae were recorded daily and subsequently analysed.

**Conclusions:** Egg masses were significantly clumped on trees and across trees. Larvae from egg masses oviposited near other egg masses coalesced into larger groups and had higher survival rates than larvae from isolated egg masses. Larvae in manipulated groups of 400 individuals fed more frequently and for longer, gained more weight, and had greater survivorship than larvae in smaller groups. These results suggest that larval foraging success serves as reinforcement for the gregarious behaviour seen in *E. s. westwoodi* larvae and also may drive selection in the oviposition preference of adult females of this species.

*Keywords*: *Eucheira socialis westwoodi*, foraging, gregariousness, kin selection, oviposition preference, sex-biased mortality, sociality.

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## INTRODUCTION

Evolutionarily, animals should engage in behaviours that maximize their relative individual fitness. Therefore, cooperative behaviour among conspecifics should not evolve due to the costs associated with intraspecific competition. Contention for limiting resources is expected to be the most intense among conspecifics, since those individuals should have the same ecological requirements and exist in the same temporal and spatial environments. However, the evolution of cooperation and sociality has occurred innumerable times within the animal kingdom in both vertebrates and invertebrates (Axelrod and Hamilton, 1981; Sachs *et al.*, 2004; Nowak, 2006). Furthermore, the degree of complexity in social behaviours varies widely among animals; for example, a flock of loosely associating birds and a pair of monogamous primates can both be considered 'social'. While repeated attempts have been made to subdivide sociality into several distinct categories such as 'subsocial' and 'eusocial', critics have argued that any subgrouping is artificial and would only serve to obscure the continuity present in sociality among animals (Michener, 1974; Costa and Fitzgerald, 1996). In contrast, others have suggested that a case by case operational definition of sociality may be necessary to ensure that it is consistently presented unambiguously and within context (Wcislo, 1997).

Although it is unclear how these social systems evolved, understanding the genetic and ecological factors that maintain social behaviour has challenged evolutionary biologists since Darwin. Specifically, when he considered the evolution and maintenance of altruistic behaviour seen in worker honeybees, he questioned how an apparently pure altruistic behaviour could persist when the individuals that displayed that behaviour never reproduced. Although initially perplexed by these behaviours, Darwin was ultimately able to overcome this problem when he expanded the concept of individual fitness to include both personal reproduction and the reproduction of relatives (inclusive fitness). These ideas have since been formalized as the theory of kin selection (Hamilton, 1964a, 1964b; Smith, 1964).

The altruistic behaviour of honeybee workers is understood using kin selection; the haplodiploid sex determination of honeybees means that workers should have higher inclusive fitness by helping their queen reproduce than they could obtain by their own reproduction (Trivers and Hare, 1976). Altruistic behaviour in humans, where individuals forego reproduction to help a sibling produce and raise a child, could also be understood using kin selection. The evolutionary maintenance of social behaviour via kin selection requires that interacting individuals have a high degree of relatedness (Michod, 1982; Queller and Strassmann, 1998). However, while many animal social systems involve interactions among family members, there are also many systems where unrelated individuals cooperate (Eberhard, 1975; Bernasconi and Strassmann, 1999; Queller *et al.*, 2000).

One of the simplest of these social systems is when a group of unrelated individuals reside together and have minimal conspecific interactions, yet there appear to be benefits to the individual for choosing to exist socially. For example, thermoregulation can be more efficient for individuals living in groups than those living in isolation (Withers and Jarvis, 1980; Du Plessis and Williams, 1994). Similarly, individuals within a group have less probability of being captured by a predator than isolated individuals (Hamilton, 1971). The evolutionary maintenance of individual behaviour in these systems can be easily understood using a cost–benefit analysis done at the level of the individual. The costs to an individual engaged in this type of social interaction should be minimal because each individual provides relatively little to the group aside from existing within the group and no specific tasks related to the group are completed.

We studied *Eucheira socialis westwoodi* (Lepidoptera: Pieridae), a pierid butterfly endemic to the Mexican highlands ranging from northern Sonora to Jalisco. Female butterflies eclose with a full complement of mature eggs, which are laid as one group of 350–400 on a single leaf of the host plant, *Arbutus xalapensis* (Ericaceae). Larvae hatch and within 3 days spin a mat of silk on the leaf. They later cooperatively spin and maintain a hollow silken nest in which they reside during the day. They feed nocturnally along silken trails and unlike most butterflies and moths, remain gregarious until pupation, which occurs within the larval nest (Underwood, 1994). In addition, the larval nest is used for thermoregulation and larval success is related to the thickness of the nest wall (Fitzgerald and Underwood, 2000). Thin-walled nests produce very few pupae compared with nests of thicker walls. Therefore, the construction and maintenance of the silken nest is necessary for survival of late instar larvae to adulthood in this species. Furthermore, mortality and time spent working on the nest are positively correlated in late instars (Underwood and Shapiro, 1999a, 1999b).

The construction and maintenance of a nest requires that a group of larvae work together. We propose that the initial evolution of sociality in *E. s. westwoodi* was probably driven by kin selection, as facilitated by the single oviposition event yielding one highly related egg mass (see Fig. 1 for an outline of *E. s. westwoodi* life history/selection mechanisms) whose members work together to construct the nest. However, it seems that the maintenance of sociality during the early larvae stage cannot be explained by kin selection alone, as females also oviposit their clutches in close proximity to other egg clutches and larval groups typically coalesce to form groups of related and unrelated larvae (Porter *et al.*, 1997). We therefore investigated the influence of group size on larval foraging efficiency and mortality as potential selection factors maintaining sociality during early larval instars in this species.

## METHODS

### *The effect of oviposition behaviour on the distribution and mortality of E. s. westwoodi larvae*

We examined the effect of female oviposition behaviour on subsequent larval distribution and mortality by following 88 egg masses from hatching until the fourth instar from August to September 2005, in El Madroño, Durango, Mexico (Highway 40, km 64). We categorized egg masses prior to hatching as either being clumped with other egg masses or oviposited in isolation. We checked egg masses and subsequent larval groups approximately every 5 days for emergence and survival. During each data collection bout, a larval group that was approximately equal to the numerical combination of previous nearby larvae groups was considered to be a coalesced group; larval groups that were not found near their last known location and also could not be accounted for in a nearby coalesced group were considered to be dead.

We analysed coalescence and survivorship data using two separate $2 \times 2$ contingency tables (chi-square) via the 'Crosstab' function in SPSS (v.17) to test for an effect of the original egg mass placement, either clumped or isolated.

### *Experimental set-up used for the manipulated tests*

The experiments described below followed the same protocol. We constructed larval groups of *E. s. westwoodi* using second instar larvae from 40 naturally occurring colonies collected

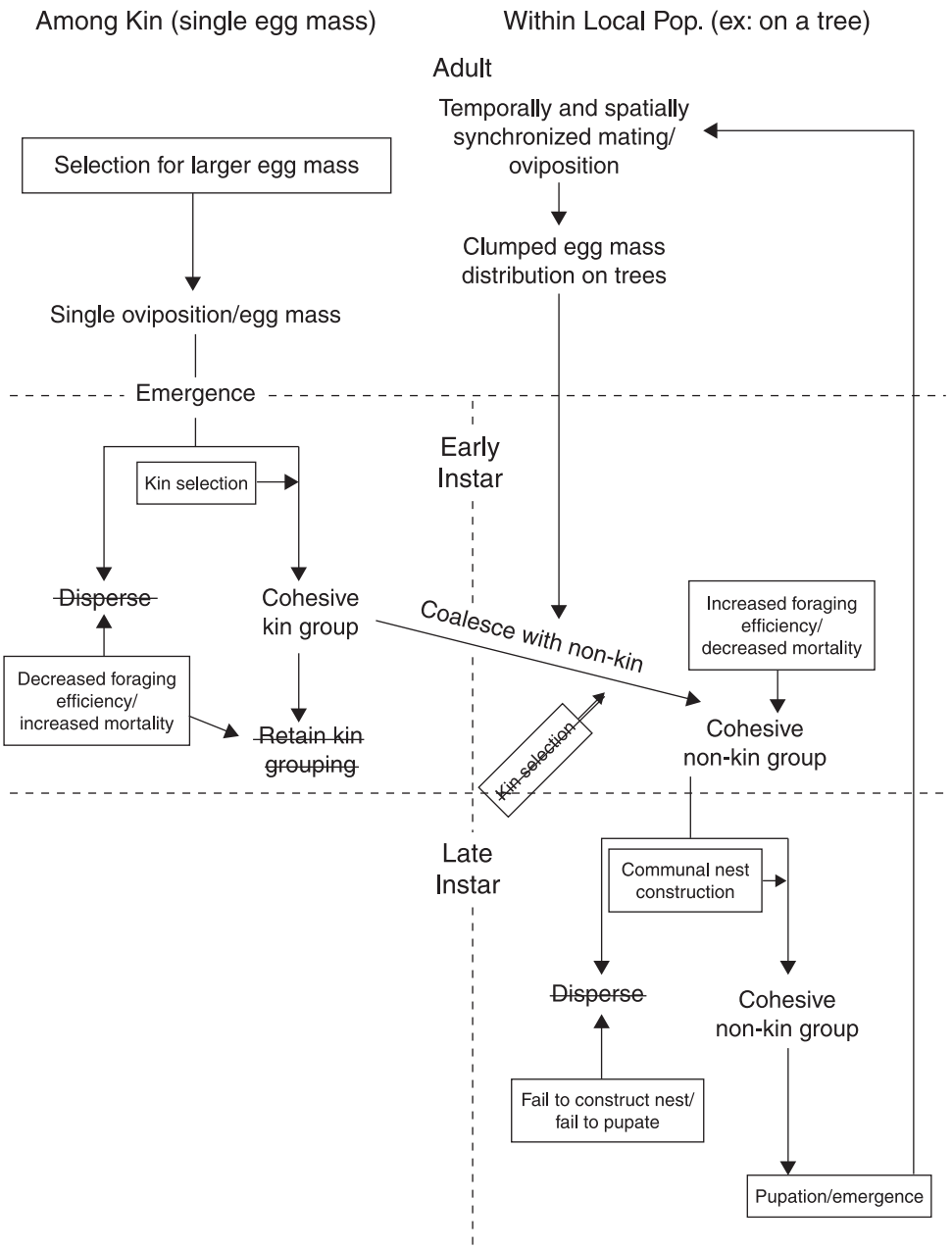


**Fig. 1.** An abstract flowchart of current and previously proposed agents of selection (boxed) acting on both the adult and larval life stage of *E. s. westwoodi*, and the consequential social behaviours produced by selection.

along Mexico Highway 40 (km 56–70). We then placed these colonies together in a plastic shoebox with host plant leaves to allow members from different colonies to mix over 48 h. Experimental larval groups were maintained on 'artificial tree' foundations (Fig. 2)


**Fig. 2.** An 'artificial tree'. The 'artificial trees' were anchored in place by a string noose under the cap treads and balanced by attaching a cloth pin to the string and the *Arbutus xalapensis* sprig. The sprigs were inserted into the centrifuge tube with water and secured with cotton balls. Larval transfer onto the sprig was facilitated by stapling the larval leaf fragments onto the leaves of the sprig.

constructed of sprigs of host plant placed in centrifuge tubes (50 or 15 mL) containing water. We replenished the host plant food source as needed. We collected all host plant sprigs from the same individual tree, as trees may vary in quality for larval development (Underwood, 1994).

We established 15 groups at each of the four treatment levels (50, 100, 200, and 400 larvae) after larvae from natural colonies had mixed. As second instar larvae were fragile and difficult to handle, we counted and indirectly manipulated larvae using only the leaf fragments that they rested on to minimize the effects of handling while constructing the experimental groups. Once the correct number of larvae was reached for the treatment size, we stapled each assembled group onto an artificial tree (Fig. 2). We then allowed the groups to acclimate for 48 h to ensure complete larval transfer onto the artificial trees from the original leaf fragments prior to data collection.

*Experiment I: effect of group size on larval feeding*

We haphazardly selected 15 individuals in ten colonies from each treatment group and marked them using a black Sharpie© permanent marker. We then recorded the activity of each marked focal individual once per hour over two identical 12-h monitoring periods on two consecutive days (13 samples per day) to assess the effect of group size on the number of larvae feeding across the four treatment levels. Three categories were established to classify the activities of the marked focal individuals: feeding, resting, and walking. We monitored a total of 40 treatment groups over the course of the experimental period.

To determine the proportion of marked larvae that were feeding, we first divided the number of marked larvae feeding at each sample time in each treatment group by the total number of marked larvae ($n = 15$); we then repeated the same calculation across all 26 sample times and all treatment groups. Finally, we arcsine transformed the percent marked larval feeding data to meet the assumption of normality.

As previous studies have identified a strong effect of time on feeding behaviour in older larvae (Underwood, 1994; Underwood and Shapiro, 1999a), we first tested for an effect of time on the feeding behaviour of marked larvae in Experiment I. Specifically, we analysed the percent marked larval feeding data with a repeated-measures one-way analysis of variance (ANOVA), treating time as the repeated variable across the 26 sample times. The results of this analysis suggested that the observed behaviours in this experiment were not influenced by time ($P = 0.887$), so we decided subsequently to conduct a one-way ANOVA to test for an effect of group size on the proportion of larvae feeding using the pooled means of the percent larvae feeding across 26 sample times. In addition, we performed multiple comparisons among treatments using Tukey's HSD (SPSS v.17).

*Experiment II: effect of group size on feeding duration*

We individually removed a total of eight groups (two at each treatment level) from the experimental room for video recording over the course of the experimental period to assess the effect of group size on the amount of time larvae spent feeding. Each group was filmed for approximately 8 h using time-lapse recording (2 s per frame: Panasonic PV-GS120 MiniDV camcorder, iMovie). During playback, we followed a haphazardly selected focal individual (we did not re-use marked larvae from Experiment I) for approximately 200 elapsed minutes (200 s of video playback) and recorded the amount of time it spent feeding, walking, and resting. We repeated this process for five larvae from each of the eight groups.

To prepare the playback dataset for statistical analysis, we first divided the amount of time each focal larva spent feeding by the total elapsed time (200 min) to calculate the proportion of time that each caterpillar spent feeding. We then applied an arcsine transformation to the percent time spent feeding dataset to meet the assumption of normality.

We analysed the percent time spent feeding data using a nested one-way ANOVA design, first nesting the percent time data for all focal larvae within the same colony into a group (by a unique ID), and then nesting the groups into respective treatment levels. We also tested for differences among groups using Tukey's HSD.

*Experiment III: effect of group size on the frequency of larval contact*

We scored the encounter frequencies of five haphazardly selected larvae from each treatment group using the same time-lapse video files from Experiment II to examine the

effect of group size on the amount of physical contact between conspecifics. We used the following criteria when scoring: (1) an encounter event was logged if any part of a conspecific touched any part of the focal individual, and (2) repeated encounters were scored only if the same conspecific larva first became completely disassociated from the focal individual before re-contact at a later time. Each focal larva was observed for 120 elapsed minutes (120 s of video playback time).

We utilized a similar nested one-way ANOVA design as described for Experiment II to analyse encounter frequency among larvae. We again tested for differences among groups using Tukey's HSD.

### *Experiment IV: effect of group size on mass per capita*

We disassembled all 'artificial trees' at the conclusion of the 10-day experimental period. To assess the effect of group size on per capita weight gain, each larval leaf fragment removed from an 'artificial tree' was first photographed and weighed to the nearest milligram; we then removed all larvae from the fragment and re-weighed the fragment alone to obtain the net larval weight. We also counted the number of larvae on the photographed fragments using ImageJ (Rasband, 1997–2008) to obtain the mass per capita by dividing the net larval weight by the larval count. We analysed the mass per capita data set using a one-way ANOVA and Tukey's HSD.

### *Experiment V: effect of group size on survivorship*

Finally, we assessed the effect of group size on larval survivorship by dividing the final larval count per treatment group (from Experiment IV) by the original treatment level (50, 100, 200 or 400 larvae) to obtain the percent survivorship. We then arcsine transformed the percent survivorship data to meet the assumption of normality and subsequently analysed the data set using a one-way ANOVA and Tukey's HSD.

## RESULTS

### *The effect of oviposition behaviour on larval distribution and mortality*

The distribution of egg masses was significantly clumped across trees ($\chi^2_{9,24} = 102.11$, $P < 0.001$). Furthermore, egg mass distribution on each tree was also clumped for 13 ($\chi^2$ value range: 110.1–2226.2, all $P < 0.001$) of 14 sampled trees ($\chi^2_{4,5} = 8.2$, $P = 0.083$).

Coalescence occurred significantly more often with larval groups originating from clumped egg masses than those from isolated egg masses ($\chi^2_{1,65} = 33.704$, $P < 0.001$). Indeed, no coalescence event was recorded for groups from isolated egg masses. Furthermore, significantly more larval groups from clumped egg masses survived until the fourth instar compared with groups from isolated egg masses ($\chi^2_{1,65} = 8.539$, $P = 0.003$).

### *Experiment I: effect of group size on larval feeding*

No significant effect of time was detected when comparing percent marked larvae feeding across the 26 sample times (Wilks' $\lambda = 0.507$, $F_{25,15} = 0.584$, $P = 0.887$). When samples were pooled across time, significantly more marked larvae from the 400 group treatment size fed compared with larvae from the other group treatment sizes ($F_{3,36} = 9.23$, $P < 0.0001$; Table 1).

**Table 1.** Results of Experiments I–V (mean ± S.E.)

| Group size | Proportion larvae feeding | Proportion time spent feeding | Mean encounter frequency | Mean mass per capita (mg) | Proportion survival |
|---|---|---|---|---|---|
| 50 | $0.167 \pm 0.017^{a}$ | $0.147 \pm 0.027^{a}$ | $22.2 \pm 1.672^{a}$ | $1.081 \pm 0.025^{a}$ | $0.803 \pm 0.042^{a}$ |
| 100 | $0.175 \pm 0.016^{a}$ | $0.118 \pm 0.024^{a}$ | $27.8 \pm 2.924^{a}$ | $1.290 \pm 0.038^{b}$ | $0.844 \pm 0.029^{a,b}$ |
| 200 | $0.152 \pm 0.016^{a}$ | $0.263 \pm 0.025^{b}$ | $84.3 \pm 3.300^{b}$ | $1.314 \pm 0.030^{b}$ | $0.875 \pm 0.025^{a,b}$ |
| 400 | $0.258 \pm 0.014^{b}$ | $0.549 \pm 0.020^{c}$ | $89.7 \pm 3.471^{b}$ | $1.313 \pm 0.039^{b}$ | $0.930 \pm 0.021^{b}$ |

*Note*: All proportional results reported here are untransformed, while associated statistical analyses were conducted on arcsine-transformed values. Different superscripts correspond to significant ($\alpha < 0.05$) pairwise groupings.

### *Experiment II: effect of group size on feeding duration*

Focal larvae from the 400 group size treatment spent significantly more time feeding compared with the three smaller group size treatments (50, 100, and 200 larvae). Larvae from the 200 group size treatment spent significantly more time feeding compared with the 50 and 100 group size treatments ($F_{3,32} = 69.19$, $P < 0.0001$; Table 1).

### *Experiment III: effect of group size on the frequency of larval contact*

Focal larvae from both the 200 and 400 group size treatments received significantly more conspecific physical contacts compared with larvae from the 50 and 100 group size treatments ($F_{3,32} = 165.49$, $P < 0.0001$; Table 1).

### *Experiment IV: effect of group size on mass per capita*

Individuals within the three larger group size treatments (100, 200, and 400 larvae) did not differ significantly in final mass (mean: $1.31 \pm 0.02$ mg), while larvae from the smallest group size (50 larvae) treatment weighed significantly less ($1.08 \pm 0.03$ mg) ($F_{3,56} = 11.31$, $P < 0.0001$; Table 1).

### *Experiment V: effect of group size on survivorship*

When comparing percent survivorship, a significantly higher proportion of larvae from the 400 group size treatment survived compared with larvae from the 50 group size treatment ($F_{3,54} = 3.09$, $P = 0.035$; Table 1).

## DISCUSSION

We investigated aspects of sociality in early instar *Eucheira socialis westwoodi*. As observed in earlier preliminary studies, individual female butterflies usually placed their egg masses near conspecific egg masses. We followed the fate of isolated and clumped larval groups from hatching through the fourth instar and found that isolated groups suffered complete mortality while clumped groups coalesced to form colonies consisting of both kin and non-kin larvae that survived. We examined whether this differential mortality could be driven by early larval foraging behaviour influenced by group size.

There has been strong past selection in *E. s. westwoodi* for ovipositional behaviours that facilitate social interactions among larvae. An adult female ecloses with a full complement

of 350–400 mature eggs that she oviposits as one cluster on a single leaf of the host plant; mating occurs rapidly following emergence, with most females ovipositing within 3 h of eclosion (Underwood, 1994). In addition, dissection of 20 adult females found only a single spermatophore per spermatheca (unpublished data) implying that females mate once, and hatchlings from a given egg mass are full sibs. Therefore, the evolution of sociality at this point and within these groups can easily be explained via kin selection. However, the logical jump to the maintenance of oviposition behaviour that results in egg mass clumps among conspecific females and the subsequent larval behaviour involving cooperation among non-kin individuals cannot be readily understood using only kin selection theory (Fig. 1).

We found that individuals from large larval groups fed more frequently, for longer periods, and gained more weight than those from small larval groups. Individual activity may have been influenced by physical contact with conspecifics; specifically, isolated individuals in small groups experienced less physical contact with nearby larvae than individuals existing within a large group. In turn, we suspect that the frequency of physical contacts may result in more frequent initiation of feeding and longer feeding bouts. Flowers and Costa (2003) found that in a behavioural analogue, *Neodiprion lecontei* (Hymenoptera: Diprionidae), individuals took significantly less time to commence feeding at a site already occupied by conspecifics than early arrival individuals at a new site. Similarly, studies on *Chlosyne poecile* (Lepidoptera: Nymphalidae) and its congener *C. lacinia* have found that both feeding rates as well as percent survival are enhanced by large group sizes during early instars (Clark and Faeth, 1997; Inouye and Johnson, 2005).

Our mass per capita results are in line those of with previous foraging behaviour studies, as an increase in feeding intensity was shown to contribute to an increase in growth rate (Fordyce, 2003). Specifically, Fordyce (2006) found that in *Battus philenor* (Lepidoptera: Papilionidae), members of large groups consumed foliage faster and experienced an accelerated development rate. Furthermore, the ability of larvae to initiate a successful feeding front on a leaf could be related to the size of the larval group. Given that the second instar larvae utilized for this study had maximum body lengths of less than 1 cm and head capsule widths of approximately 1 mm, it is clear that individual larvae would have a difficult time engaging and initiating feeding on a much larger leaf. In fact, young larval feeding groups tend to 'skeletonize' leaves, leaving behind the tough fibrous venations, whereas later instar larvae are able to consume the entire leaf minus the main vein. Mechanistically, large feeding groups have been shown to increase feeding efficiency in other insect systems by overcoming the toughness in leaf tissues exhibited by some plants (Benrey and Denno, 1997; Fordyce, 2006).

In addition to the effects on differential early instar foraging success/survivorship as a result of group size as detected in this study, previous work reported that later *E. s. westwoodi* colonies differed in quality/eclosion success with respect to the sex ratio of its occupants. Specifically, *Eucheira* has a male-biased primary sex ratio thought to be caused by meiotic instability (Underwood *et al.*, 2005) with a mean of 70% male at hatching and egg masses varying from 50 to 90% male (Underwood and Shapiro, 1999b). In most diploid species, the evolutionarily stable strategy is one of parity because the rarer sex will always enjoy the greatest reproductive success (Fisher, 1930). The variation in sex ratio across egg masses in *E. s. westwoodi* implies that male-biased larval groups enjoy greater fitness than non-biased groups. Larvae remain social until pupation and this sociality has costs at least during later instars. Previous studies using fifth and sixth instar larvae found that male larvae spun more silk on the larval nest than females and larval mortality was male-biased above that

predicted given a male-biased sex ratio (Underwood and Shapiro, 1999a, 1999b). Furthermore, Yayalar (2009) found that individual male larvae that spent more time spinning silk on the nest had a higher probability of mortality than larvae that spun less. Minimally, the nest functions in thermoregulation by providing a cool microclimate during sun-intensive days (Fitzgerald and Underwood, 2000) and the quality of the nest (nest wall thickness) was found to be positively correlated with larval survivorship (Underwood, 1994). As colonies at this stage typically comprise both kin and non-kin larvae (Porter *et al.*, 1997), the maintenance of sociality through increased inclusive fitness at this stage in the life cycle is unlikely.

However, the evolution of cooperation can theoretically occur despite obvious genetic constraints (e.g. Platt and Bever, 2009; Lehmann and Rousset, 2010). Specifically, in populations with little dispersal, the probability of related individuals interacting is enhanced (viscous populations). In *E. s. westwoodi*, adult females have limited dispersal capabilities and are largely blown downwind from their natal nests (Underwood, 1992), which enhances the probability of sisters ovipositing on the same tree. Moreover, selection can favour groups of cooperating individuals over non-cooperative individuals if the productivity of these groups leads to a greater contribution of offspring to the next generation (Platt and Bever, 2009). As Wcislo (1997, p. 11) suggested, 'the most evolutionarily relevant event was an initial association of conspecifics, because without its occurrence the evolutionary elaboration of societies would be impossible'.

In summary, female fitness is optimized by clumping egg masses near those of conspecifics because of the influence larval group size has on the foraging efficiency and subsequent survival of young larvae. As larvae mature and contribute silk to the larval nest, sociality is reinforced as the nest plays an important role in survival via thermoregulation. The male-biased sex ratio results in an asymmetry in mating success between males and females whereby many males will go unmated but nearly all or all females will be successful, decreasing the costs of male-specific larval behaviour and mortality associated with sociality. Hence, the maintenance of sociality in this system arguably involves both kin selection and multi-level selection among unrelated individuals within a local population.

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