Social pseudoscorpion nest architecture provides direct benefits to group members and rivals the efficiency of honey bees

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Abstract. Animals may build nests socially to minimize the energy required for nest construction. *Paratemnoides* spp. pseudoscorpions evolved sociality independently from all other social groups, and colonies create silken multi-chambered nests in which they molt and raise young, analogous in form to the nests of some wasps and bees. Here we describe these nests and examine pseudoscorpion construction efficiency. Silk is generally energetically expensive and as such, we hypothesized that *P. elongatus* build nests of a structure that minimizes silk use, thereby maximizing nest construction efficiency. We measured the number of nest chambers, their perimeter, and their area, for 31 nests, calculated several metrics of nest architecture, and developed five alternative mathematical models describing other possible nest geometries. We found that real social pseudoscorpion nests are constructed with high efficiency, measured as wall length per internal area, approaching that of mathematical optima. We also found that these nests use less silk per capita than if the same chambers were built separately, i.e., if they were solitary. This indicates a direct benefit to group members. We compared observed nest architecture with five mathematical models of nest geometry and found that pseudoscorpion construction efficiency outperformed all non-cooperative models and rivaled that of a cooperative one approximating the honeycomb conjecture - a mathematical proof describing the most efficient way possible to divide a 2-dimensional plane. In summary, social pseudoscorpions design group nests with multiple chambers in a way that minimizes wall length per internal area and approaches the efficiency of honey-bee-like hexagon constructcion.

Keywords: Bioconstruction, cooperation, nest construction, *Paratemnoides*, silk

https://doi.org/10.1636/JoA-S-21-017

Cooperative construction, where individuals collectively build structures, is seen across Animalia. Social species of mammal and reptile cooperatively construct burrows (e.g., Šumbera et al. 2012; Fruth et al. 2017; McAlpin et al. 2011), birds cooperatively build nests (e.g., Zyskowski & Prum 1999; Hansell 2005; Walsh et al. 2010), as do insects (e.g., DiRienzo & Dornhaus 2017; Tschinkel 2004; Wille & Michener 2016), and arachnids (e.g., Agnarsson et al. 2006); and a diversity of microbial life cooperatively alter their environment in the form of biofilms and bioflocculants (e.g., Stoodley et al. 2002; Smukalla et al. 2008; Oliveira et al. 2015; Kovács & Dragoš 2019).

The construction of cooperative structures was once thought to imply that individuals had an understanding of the overall construction design, but we now understand that many complex cooperative structures are constructed via self-organization, without a leader or template, and that stigmergy may play a large role in coordinating individuals (Grassé 1959; Denebourg & Goss 1989; Bonabeau et al. 1997; Theraulaz et al. 1999). In the context of cooperative construction, stigmergy is an indirect communicative process where the structures built by individuals inform group members of where to build next, resulting in a self-organized and distributed (i.e., not centralized or hierarchical) process of complex nest construction (Grassé 1959). Research on many social insects has shown that the colony can construct nests with stigmergic cues alone, requiring no direct communication (Khuong et al. 2016; Perna & Theraulaz 2017).

Cooperative construction has evolved several times independently across life (Schmitz & Moritz 1998; Armitage 1999; Danforth 2002; Lubin & Bilde 2007; While et al. 2009). For example, phylogenetic analyses show that sociality and cooperative construction evolved independently twice among vespid wasps (Schmitz & Moritz 1998; Hines et al. 2007) and marmots (Kruckenhauser et al. 2002), three times in halictid bees (Danforth 2002), and over 20 times among spiders (Agnarsson 2002; Agnarsson et al. 2006; Salomon & Lubin 2007; Majer et al. 2018).

Building cooperatively can reduce per capita costs of construction. For example, spiderlings of a pholcid species cooperatively build webs, but cooperative webs catch fewer prey per capita compared to solitary ones (Jakob 1991). However, cooperative webs require only a fraction of the per capita silk production of solitary webs. Spiderling groups forced to use more silk in experiments were smaller and grew slower than controls, suggesting that the cost of food competition is worth the benefit of shared web construction (Jakob 1991). Indeed, the energy required to build structures, either by producing materials or acquiring them in the environment, has been shown to have reproductive fitness costs in several species (e.g., Mikheyev & Tschinkel 2004; Moreno et al. 2010; Riehl 2010; Mainwaring & Hartley 2013).

Among arachnids, cooperative construction and sociality are rare but widely interspersed across taxa; cooperatively constructing spiders have evolved independently at least 20 times across seven disparate families (Agnarsson et al. 2006; Salomon & Lubin 2007; Majer et al. 2018). Sociality in other arachnid orders is poorly understood, but has been observed among species of mite, scorpion, and pseudoscorpion. In particular, scorpion offspring of *Heterometrus* (Ehrenberg, 1828) help maintain and expand burrows built by their mother (Shivashankar 1994); *Stigmaeopsis* mites collectively construct

Figure 1.—Photos of nests of the social pseudoscorpion *Paratemnoides elongatus*. Top row: *ex-situ* nest structures illustrating how individuals use nests. Young, gravid, and molting individuals take refuge in the cells, while adults surround the nest. Bottom rows: only *in-situ* nests were included in this study. Nests are composed of silken cells adjoined. Passages are bored through walls which allow movement between cells.

a large silken roof under which social groups defend themselves (Mori & Saito 2005); and *Paratemnoides nidificator* (Bazlan, 1888), a congener of this study's focus, engages in cooperative prey capture and offspring care, and shows high levels of sociality (Tizo-Pedroso & Del-Claro 2005, 2007, 2011, 2018).

Here, we present the complex nest architecture of the social pseudoscorpion *Paratemnoides elongatus* (Banks, 1895) for the first time. *Paratemnoides* Harvey, 1991 pseudoscorpions construct silken, multi-chambered nests connected with passageways, that, unlike other arachnid structures, appear remarkably similar in geometry to nests of bees and wasps (Fig. 1), but evolved independently from other groups (Moura et al. 2018). The social behavior of *P. elongatus* was qualitatively described (Brach 1978), as was their cooperative foraging behavior (Zeh & Zeh 1990). The species has been

included in a general survey of pseudoscorpions (Brach 1979) and was mentioned as occurring phoretically on fireflies (Lloyd & Muchmore 1975). *Paratemnoides elongatus* occur in groups around silken nests and will cooperatively capture prey (Brach 1978; Zeh & Zeh 1990). The nest architecture of pseudoscorpions, however, has never been empirically examined.

We investigated the nest architecture of social pseudoscorpions, with specific interest in understanding how pseudoscorpions may benefit from reduced construction costs of cooperative nest building. In particular, we measured the length of silk wall required to construct actual nests and compared them to geometric expectations of nest construction, including five alternative models of nest construction that vary in silk use efficiency and design.

Table 1.—Pseudoscorpion nest architecture metrics that we measured or calculated for further analysis.

Variable	Symbol	Unit	Calculation
Nest area	a	mm^2	Image processing
Nest perimeter	p	mm	Image processing
Major axis	m	mm	Image processing
Roundness	R	-	$R = 4a/\pi m^2$
Circularity	C	-	$C = 4\pi(a/p^2)$

METHODS

Study species.—Pseudoscorpions are a poorly understood group of arachnids, which includes more than 3500 species, over half of which have been described in the last 50 years (Weygoldt 1969). Pseudoscorpions produce silk from their chelicerae and many species produce venom from their pedipalps, which they use to subdue prey.

All known species molt three times after hatching, and during this process use a silken refuge during termed a moltarium (Weygoldt 1969). Pseudoscorpions in general have a dorso-ventrally flattened body morphology, enabling many species to seek refuge in narrow crevices, including those between the pages of library books (Aristotle 322 BCE, translated in Aristotle et al. 1878). Moltaria are constructed with silk that pseudoscorpions use to span the crevice gap. They form a circular wall around themselves and generally apply a thin layer of silk to the moltarium floor. They then enter torpor and are immobile during the molting process. Pseudoscorpions are at higher risk of infection and predation when undergoing this process (Weygold 1969; Del-Claro & Tizo-Pedroso 2009).

Most female pseudoscorpions also use silk to form brood chambers. Pseudoscorpions mate via spermatophore, and females produce eggs externally but attached to their ventrum. Once laid, the eggs are supplied with nutritive fluid produced by the female throughout development (Weygoldt 1969). Embryonic pseudoscorpions are equipped with a pumping organ—a mouth structure that enables the uptake of nutritive fluid. This structure is lost in adults, although retained pedomorphically in some species to enable postembryonic nursing (Weygoldt 1969). In at least a few species, the nutritive fluid is supplied early in development, the egg sac is detached from the body, and the female stays enclosed in a brood chamber with eggs until offspring disperse (Weygoldt 1969). Still other species use silk for a variety of less common purposes, like during mating, courtship, and by males to attract females (Weygoldt 1969).

Nest collection and imaging.—We collected nests of social pseudoscorpion *Paratemnoides elongatus* from exfoliating bark layers of slash pine trees (*Pinus elliottii*) at Archbold Biological Station in Venus, FL (27.183, −81.353) in December and January 2019. We digitally imaged bark pieces containing nests of *P. elongatus* alongside a millimeter scale using a Lumix DMC-GH3 digital camera with an Olympus 60mm lens mounted on a copy stand to record images directly perpendicular to the bark for accurate measurement. We excluded nests where we were unable to distinguish nest structures due to damage or age, with a final sample size of $n =$ 30 nests.

Nest roundness and circularity.—Nests are made up of a number of individual cells (Fig. 2). Cells are made one at a time by a single pseudoscorpion (pers. obs.). We recorded several metrics of each nest and constituent cells using ImageJ 1.52a, to the nearest pixel. We converted pixel values to millimeters, resulting in ca. 0.001 mm precision. We measured the perimeter and area of both entire nests and individual cells of which nests are composed. With these measurements, we calculated two indices as indicators of the level of silk efficiency pseudoscorpions use: roundness and circularity (*sensu* Takashimizu & Iiyoshi 2016; Table 1). We calculated roundness (R) as,

$$R = 4a/\pi m^2$$

where a is the area of the nest, m is the major axis—the longest possible line segment across the nest. A perfect circle, which is the shape that is most silk-efficient (i.e., minimum silk perimeter with maximum cell area) would have $R = 1$, with lower values indicating a shape that is less round than a circle. We calculated circularity (C; Table 1) as,

$$C = 4\pi a/p^2$$

where p is the observed perimeter. As such, roundness compares the observed nest area with a perfect circle with consideration of aspect ratios, whereas circularity compares the observed nest area with a matching perimeter. Both measures are estimates of how a shape deviates from a circle - roundness can be thought of as the level of elongation, whereas circularity can be imagined as the sinuosity of the silk perimeter. We consider a cell or nest of high silk-use efficiency if it uses minimal silk for a given internal area. As such, a cell or nest with high silk use efficiency has minimal silk walls while maximizing area.

Comparative nest models.—We developed five alternative models for nest architecture to compare silk use efficiency with observed nests (Table 2): noncooperative nests, noncooperative nests with hexagon cells, cooperative nests with hexagon cells, noncooperative circular cells, and both cooperative and noncooperative plastic cells, which are a hybrid of hexagons and circles (details below). Models are termed *cooperative* if cells share silk walls, as occurs in *P. elongatus*. *Noncooperative* models are calculated without shared walls, as if cells were built independently. Mathematical derivations for model equations are provided in Supplement Materials (online at https://doi.org/10.1636/JoA-S-21-017.s1).

Noncooperative observed model.—We estimated the silk use of nests if pseudoscorpions did not share nest walls, but cell structures matched observed nests that we photographed and measured by totaling the perimeter (p) of individual cells in each nest. This results in double-counting shared walls. Thus, the noncooperative observed model estimates the wall-length of silk that would be required if the species were not social, i.e.,

$$\sum_{i=1}^{n} p_i$$

where p_i is the perimeter of cell i.

Hexagons models.—Mathematically, a regular hexagonal grid approximating a honey bee hive is the most efficient way
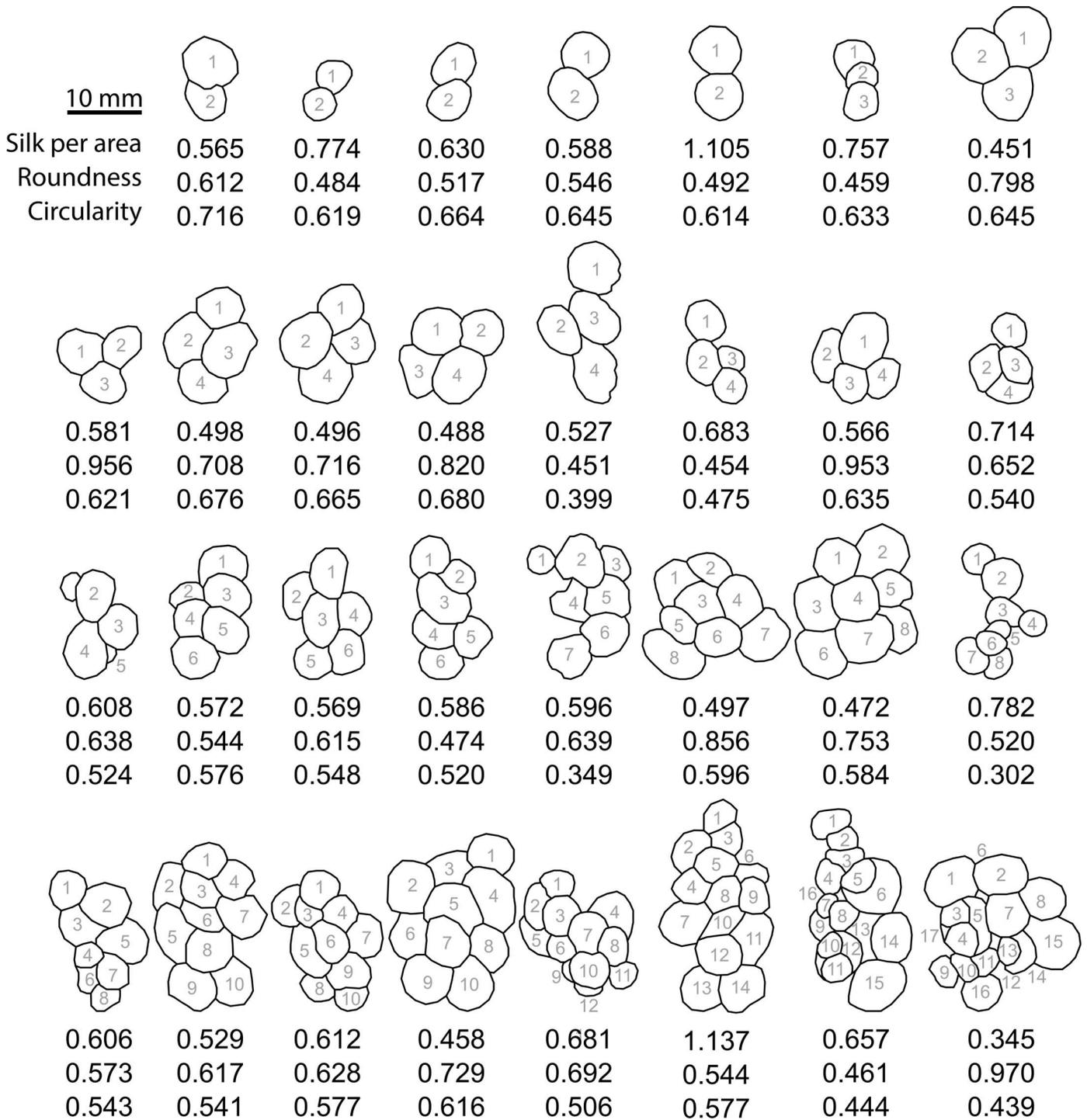
Figure 2.—Traces, cell counts, silk per area, roundness, and circularity for all nests measured, with 10mm scale.

of dividing a plane into cells of equal area with the least total perimeter (termed the Honeycomb Conjecture; Hales 1999). As such, we would expect the most efficient (in terms of using the least construction material per area) multi-celled nests to follow a hexagonal shape. Many bee and wasp species build nests of hexagonal cells consistent with this. In doing so, colonies optimize efficiency by limiting construction materials, just as mathematics would predict (for examples see Jeanne

1975). This hexagon approach provides the colony-level benefit of minimizing overall construction material, and also an individual-level benefit, since each cell can reuse the walls of others.

Noncooperative hexagon model.—The noncooperative hexagon model estimates the silk use for a nest made of hexagonal cells but noncooperatively, such that hexagons do not share walls. The total building material required for solitary,

Table 2.—Models used as comparison for observed pseudoscorpion nest architecture. All model estimates are based on the area of observed pseudoscorpion nests. p and a are the perimeter and area of the ith cell.

Nest Model	Equation	Silk length…	Illustration
Noncooperative Observed	$$\sum_{i=1}^{n} p_i$$	…of observed nests without wall sharing.	
Noncooperative Hexagon	$$\sum_{i=1}^{n} 2\sqrt{2}\sqrt[4]{3}\sqrt{a_i}$$	…if cells were regular hexagons.	
Noncooperative Plastic	$$\sum_{i=1}^{n} 2\sqrt{\pi a_1} + \frac{1}{3}\sqrt{a_2}\left(\sqrt{2} + \sqrt[4]{3} + 5\sqrt{\pi}\right) + \frac{2}{3}\sqrt{a_{3-6}}\left(\sqrt{2} + \sqrt[4]{3} + 2\sqrt{\pi}\right)$$	…if cells were circles with flat wall where they adjoin.	
Noncooperative Circle	$$\sum_{i=1}^{n} 2\sqrt{\pi a_i}$$	…if cells were circles.	
Cooperative Hexagon	$$\sum_{i=1}^{n} \frac{\sqrt{2}\sqrt{a_1}}{3^{3/4}} + \frac{5\sqrt{2}\sqrt{a_2}}{3^{3/4}} + \frac{4\sqrt{2}\sqrt{a_{3\ldots n}}}{3^{3/4}}$$	…if cells were regular hexagons.	
Cooperative Plastic	$$\sum_{i=1}^{n} 2\sqrt{\pi a_1} + \frac{5\sqrt{\pi a_2}}{3} + \frac{4\sqrt{\pi a_{3\ldots n}}}{3}$$	…if cells were circles that flatten when adjoined.	

noncooperative hexagons equal to the cell areas of each nest can be calculated as,

$$\sum_{i=1}^{n} 2\sqrt{2}\sqrt[4]{3}\sqrt{a_i}$$

where a is the area of cell i. The noncooperative hexagon nest model is also calculated without shared walls but uses observed cell area to convert the observed shape of cells into hexagons, akin to the cells of bee and wasp nests (Table 2).

Cooperative hexagons model.—In this model, the first cell to be created will have six walls as in the noncooperative hexagon model, but the second cell can use one of the walls of the first. Thus, the second cell costs 5/6 of the first. Similarly, the second and all cells following can use two existing walls, thereby having a cell cost of 2/3. Thus, we estimate the silk required to build a nest under the cooperative hexagon model as,

$$\sum_{i=1}^{n} \frac{\sqrt{2}\sqrt{a_1}}{3^{3/4}} + \frac{5\sqrt{2}\sqrt{a_2}}{3^{3/4}} + \frac{4\sqrt{2}\sqrt{a_{3\ldots n}}}{3^{3/4}}$$

where a is the area of cell i. While the first cell in nest construction has the same cost of a solitary nest, the second cell can reuse the existing wall of the first cell, thereby reducing construction cost to the individual making the cell. In the case of hexagonal cells, the second cell only requires 5/6 of the building material because one wall of the hexagon can be made of an already existing cell wall (Table 2). Third and all cells thereafter require only 2/3 of the building material, as they need only construct four new hexagon walls against two that already exist.

Noncooperative circles model.—At the individual level however, a regular circle, not a hexagon, minimizes construction materials. This is simply because a circle has the smallest perimeter:area ratio of any two-dimensional form. A single hexagon requires more building material (measured as length of cell wall) compared to a solitary circular nest of equal volume. The additional building material required for individuals to construct hexagons instead of circular cells of equal area increases sublinearly with area, such that,

$$y = 2\sqrt{a}(\sqrt{2}\sqrt[4]{3} - \sqrt{\pi})$$

where a is a given area and y is the additional perimeter required for a hexagon cell compared to a circle. The total perimeter of circular cells of equal area to those in observed nests can be calculated as,

$$\sum_{i=1}^{n} 2\sqrt{\pi a_i}$$

Cooperative plastic model.—Consider an incipiently or facultatively solitary species that constructs circular cells (as is most efficient for the individual) but will take advantage of existing walls made by others if the opportunity arises. How much existing wall should an adjoining cell utilize? The more existing wall used, the less new wall that is needed for construction, thereby conserving construction costs. However, since the existing wall is circular, using too much wall will result in a concave shape that reduces both the circularity of the new cell and its area. We can calculate the area of a cell that uses the concave wall of an adjoining cell. Assuming circular cells arranged in a hexagonal pattern (per the Honeycomb Conjecture; Hales 1999), the reduced cell area as a consequence of using an existing wall can be calculated as,

$$a - \sqrt{\frac{a^2}{\pi}\left(\frac{3}{\pi} - sin\left(\frac{3}{\pi}\right)\right)}$$

In many systems, opposing forces can flatten the concave wall of the adjoining cell, thereby creating a straight wall much like that of a hexagon. For example, two soap bubbles (or cells) of equal size next to each other have a flat facet between them because their surface tension is equal. If we assume a similar process occurs with biological multi-cell cooperative structures, for example the movement of larvae adding outward pressure to cell walls, then the construction material use efficiency of multi-celled cooperative structures might best be modeled by combining ideas of circle packing to maximize usable space, the honeycomb conjecture to minimize total perimeter, and facet-sharing principles from physics to transition between the two. In this sense, the ideal cell is circular, but with the ability to form flat, hexagon-like walls dynamically and as an emergent, collective property. If this were the case, then the total length of construction material required by all individuals to construct a nest of cells with a given area can be calculated as,

$$\sum_{i=1}^{n} 2\sqrt{\pi a_1} + \frac{5\sqrt{\pi a_2}}{3} + \frac{4\sqrt{\pi a_{3...n}}}{3}$$

where cell perimeter of the first cell (1) is calculated from its area and requires a full perimeter be built; the second cell reduces construction costs by ⅙ by using a portion of the first cell; and all cells thereafter reduce construction costs by ⅓. The total loss of cell area due to cooperation in this nest model would be,

$$\sum_{i=3}^{n} 2\frac{(2\pi - 3\sqrt{3})^2 a_2}{24\pi} + \frac{(2\pi - 3\sqrt{3})^2 a_{3...n}}{24\pi}$$

Note that the first cell is not counted in this case because it does not sacrifice area to cooperate. Organisms that used a

strategy like this would reduce construction costs by cooperating, but also produce efficient solitarily nests. Nests are often constructed of flexible materials amenable to this shift in structure.

The cooperative plastic model uses circular cells except when adjacent to another cell, in which case a flat edge is formed akin to one size of a hexagon. This model has the benefit of being maximally efficient (in terms of construction cost per area) when constructed solitarily, while still benefiting from shared walls when they are available.

$$\sum_{i=1}^{n} 2\sqrt{\pi a_1} + \frac{5\sqrt{\pi a_2}}{3} + \frac{4\sqrt{\pi a_{3...n}}}{3}$$

Noncooperative plastic model.— The noncooperative plastic model is the cooperative plastic model with the added costs of no wall sharing. Like the Cooperative plastic model, cell walls are circular unless they adjoin another cell, in which case the wall is flat as in the hexagon models. A noncooperative plastic model can be calculated as an alteration to the cooperative plastic model by adding the cost of hexagon edges where walls would share,

$$\sum_{i=1}^{n} 2\sqrt{\pi a_1} + \frac{5\sqrt{\pi a_2}}{3} + e_2 + \frac{4\sqrt{\pi a_{3...n}}}{3} + 2e_{3...n}$$
$$= \sum_{i=1}^{n} 2\sqrt{\pi a_1} + \frac{5\sqrt{\pi a_2}}{3} + \frac{\sqrt{2a_2}}{3^{3/4}{}_2} + \frac{4\sqrt{\pi a_{3...n}}}{3} + 2\frac{\sqrt{2a_{3...n}}}{3^{3/4}}$$

which simplifies to,

$$\sum_{i=1}^{n} 2\sqrt{\pi a_1} + \frac{1}{3}(\sqrt{2}\sqrt[4]{3} + 5\sqrt{\pi})\sqrt{a}$$

Statistical analysis.—We estimated the relationship of cell and nest area and perimeter by linear regression, and examined how these results compare to a generated dataset of the minimal perimeter-area relationship but with identical sample size and perimeters using the model equations and via t test. We also investigated whether nest circularity or roundness changed with the number of cells via linear regression. Further, we tested the relationship between the number of cells in a nest with nest identity as a random effect and the nest and cell perimeter:area ratio (a measure of silk use efficiency) to understand how this relationship changes with nest size. Last, we used pairwise, paired t tests to compare alternative models of nest construction with observed metrics. We performed all analyses in R version 4.0.3 (R Core Team 2021).

RESULTS

Paratemnoides elongatus built silken nests between layers of exfoliating bark of several tree species, but were most commonly found between layers of slash pine bark (*Pinus elliottii*; Fig. 1). The wall height of these nests generally ranged from < 1mm to ca. 3 mm depending on the topography of both bark layers. Nests were more often found lower (< 0.5m) on trees, where moisture from the ground contributed humidity to the microhabitat. Pseudoscorpions occurred in groups associated with nests, most often with juveniles, molting individuals, and brooding females inside the nest,
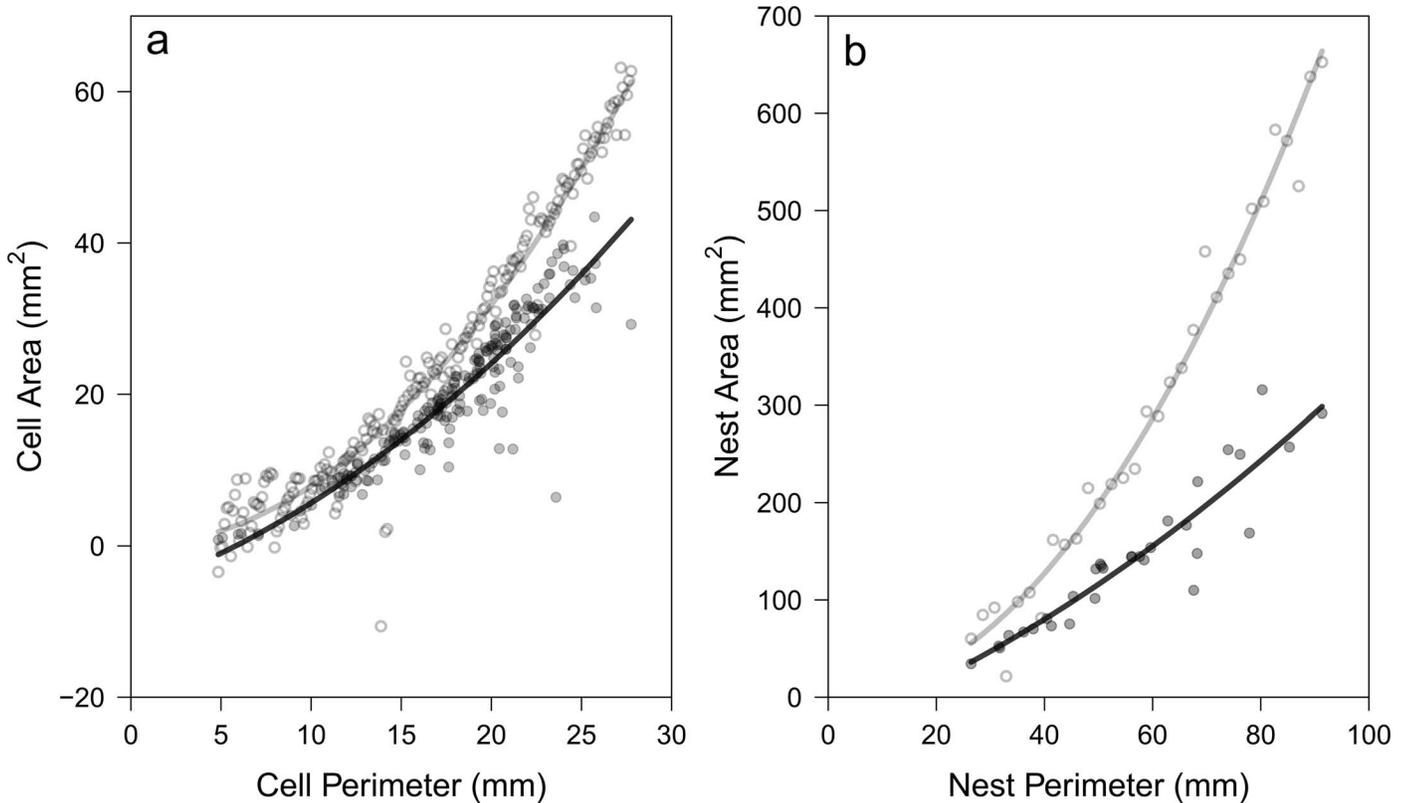
Figure 3.—Correlation of pseudoscorpion (a) cell and (b) nest perimeter (x axis) and area (y axis). Thin line represents the maximum area:perimeter ratio for a circle of a given circumference ($y=x^2/4\pi$). Dots further from the thin line indicate a less circular shape. The thick lines represent the slope from a linear regression. Perimeter-area relationships were both significant (a: slope $= 1.95 \pm 0.06$, $F_{1,195} = 1106$, $P < 0.001$, $R^2 = 0.85$; b: slope $= 4.07 \pm 0.30$, $F_{1,28} = 187.0$, $P < 0.001$, $R^2 = 0.87$). The slope of nests was about twice that of cells, and thus more closely matches the ideal (perimeter-minimizing) line.

and other adults surrounding the outside. *Ex situ* nests confirmed these findings (Fig. 1).

The nests we collected ($n = 31$) had a mean $\pm$ SEM of 6.42 $\pm$ 0.78 cells (range: 2–17), with an overall perimeter of 55.66 $\pm$ 3.06 mm, area of 142.37 $\pm$ 13.21 mm^2 and total silk wall length of 81.22 $\pm$ 6.93 mm (Fig. 2). Roundness ranged from 0.45 for elongate nests to 0.79 for rounder shapes, and circularity ranged from 0.45–0.79, with higher numbers for less circuitous perimeters (Fig. 2).

Both nest and cell perimeter were predicted by cell area. The slope of nests (slope $= 4.07 \pm 0.30$, $F_{1,28} = 187.0$, $P < 0.001$, $R^2 = 0.87$; Fig. 3) was about twice that of cells (slope $= 1.95 \pm 0.06$, $F_{1,195} = 1106$, $P < 0.001$, $R^2 = 0.85$). This makes sense, given that the relationship between perimeter and area of a circle is $p = 2\pi\sqrt{a_i/\pi}$, and nests are necessarily always larger than cells. Both nests ($t_{296} = 3.34$, $P < 0.001$) and cells ($t_{30.02} = 8.49$, $P < 0.001$) showed significant departures from an ideal dataset with maximum possible perimeter:area relationship, but with identical residuals, sample size, and perimeters. Nests also showed a larger departure from the optimal perimeter:area ratio relative to cells (Fig. 3).

Nest circularity declined with the number of cells in the nest (slope $\pm$ SEM$= -0.010 \pm 0.003$, $F_{1,29} = 6.904$, $P = 0.014$, $R^2 = 0.16$; Fig. 4a), but a trend was not detected for roundness ($F_{1,29} = 0.64$, $P = 0.430$; Fig. 4b). Further, the best-fit slope of roundness and circularity did not differ from zero ($F_{1,29} =$

1.90, $P = 0.179$). The number of cells had a negative relationship with nest perimeter:area ratio (slope $\pm$ SEM: -0.017 $\pm$ 0.004, $F_{1,28} = 17.84$, $P < 0.001$, $R^2 = 0.36$; Fig. 4c), but a positive relationship after including the number of cells as a fixed effect and nest identity as a random effect ($F_{1,28} = 15.06$, $P < 0.001$; Fig. 4d).

The observed silk use was significantly less than all noncooperative models, indicating that social nest building may serve to save on silk costs. Observed silk use was outperformed by the cooperative plastic model but not significantly different from the cooperative hexagon models, where the latter is similar to honey bee cell architecture, indicating that pseudoscorpion architecture is similarly efficient in material use as honey bees (Fig. 5; Table S1, online at https://doi.org/10.1636/JoA-S-21-017.s1).

DISCUSSION

We found that social pseudoscorpions' cooperative construction efficiency rivals that of honey bees, and social nests use considerably less silk compared to equivalent nests of solitary individuals. This suggests a direct benefit to cooperative nesting and illustrates the construction efficiency of cooperative pseudoscorpion nests.

Nest construction efficiency rivaled that of the honeycomb conjecture—a mathematical proof that a hexagonal pattern
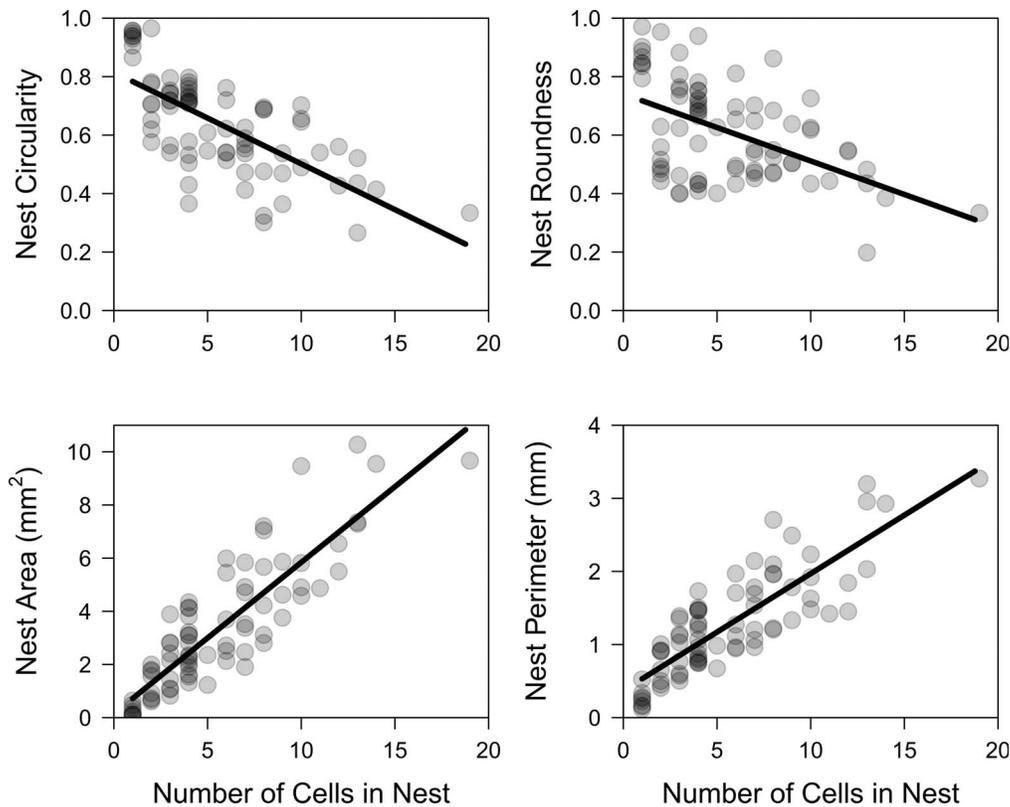
Figure 4.—Linear regressions between the number of cells and (a) nest circularity (slope $\pm$ SEM= -0.010 $\pm$ 0.003, $F_{1,29} = 6.904$, $P = 0.014$, $R^2 = 0.16$); (b) nest roundness ($F_{1,29} = 0.64$, $P = 0.430$); (c) the nest perimeter:area ratio (slope $\pm$ SEM: -0.017 $\pm$ 0.004, $F_{1,28} = 17.84$, $P < 0.001$, $R^2 = 0.36$), and (d) the perimeter:area ratio of each cell ($F_{1,197} = 22.57$, $P < 0.001$, $R^2 = 0.098$; with nest identity as a random efffect: $F_{1,28} = 15.06$, $P < 0.001$).

divides a two-dimensional plane in equal portions with the least total perimeter possible—and was outperformed by our combined cooperative plastic model, where cells are circular to maximize individual efficiency but flatten when adjoined in a hexagonal grid to maximize collective efficiency. However, pseudoscorpion cells are much less regularly shaped and geometric than modeled forms. This could be because pseudoscorpions benefit from having flexibility in cell design to accommodate the bark substrate between which they form nests. Honey bees and other social Hymenoptera that construct cooperative nests oftentimes have cells that do not make contact with the environment, but only other cells. This would reduce any benefit for accommodating variation in substrate and allow a more canonized cell geometry.

Alternatively, pseudoscorpion nests may simply not require such high efficiency in nest design. Unlike the social hymenopterans that are holometabolous, pseudoscorpions hatch from eggs in their adult form (similar to ametabolous insects; Weygoldt 1969). Juvenile pseudoscorpions lack sclerotized exoskeletons and are thus less protected relative to adults. Unlike social insects however, juvenile pseudoscorpions are motile and can leave the cell, and as such may not require specific microenvironmental conditions for development relative to animals like honey bees, for example, which can suffer developmental effects from even small changes in temperature (Simpson 1961; Perz & Aron 2020). As such, social pseudoscorpions may be able to develop under a wider

range of conditions, and this could be reflected in pseudoscorpion cell architecture.

Circularity (departure from a perfect circle by perimeter comparison) and roundness (departure also accounting for aspect ratio) did not correlate with each other, but circularity decreased with the number of cells composing a nest. This makes intuitive sense, as each cell added can decrease the lower limit of circularity by forming nests that are more elongate than those with fewer cells. This is also consistent with the increased variance seen among nests with more cells, not only for circularity, but also area and perimeter. Further, the number of cells had a negative relationship with the nest perimeter:area ratio, but a positive relationship with cell perimeter:area ratio (Fig. 4), suggesting a superlinear relationship between nest perimeter and area (as in Fig. 3).

Circles are packed efficiently (in terms of maximizing circle density or minimizing wasted space) when they assume a hexagonal formation. While the optimal solitary nest formation is a regular circle, the optimal cooperative nest construction is adjoining hexagons. As such, we expected *P. elongatus* nests to best approximate this form. We found that the observed nest structure used significantly less silk per unit area than all noncooperative models but was outperformed by the cooperative plastic model. Further, we did not find a difference between the cooperative hexagon model and observed measurements.
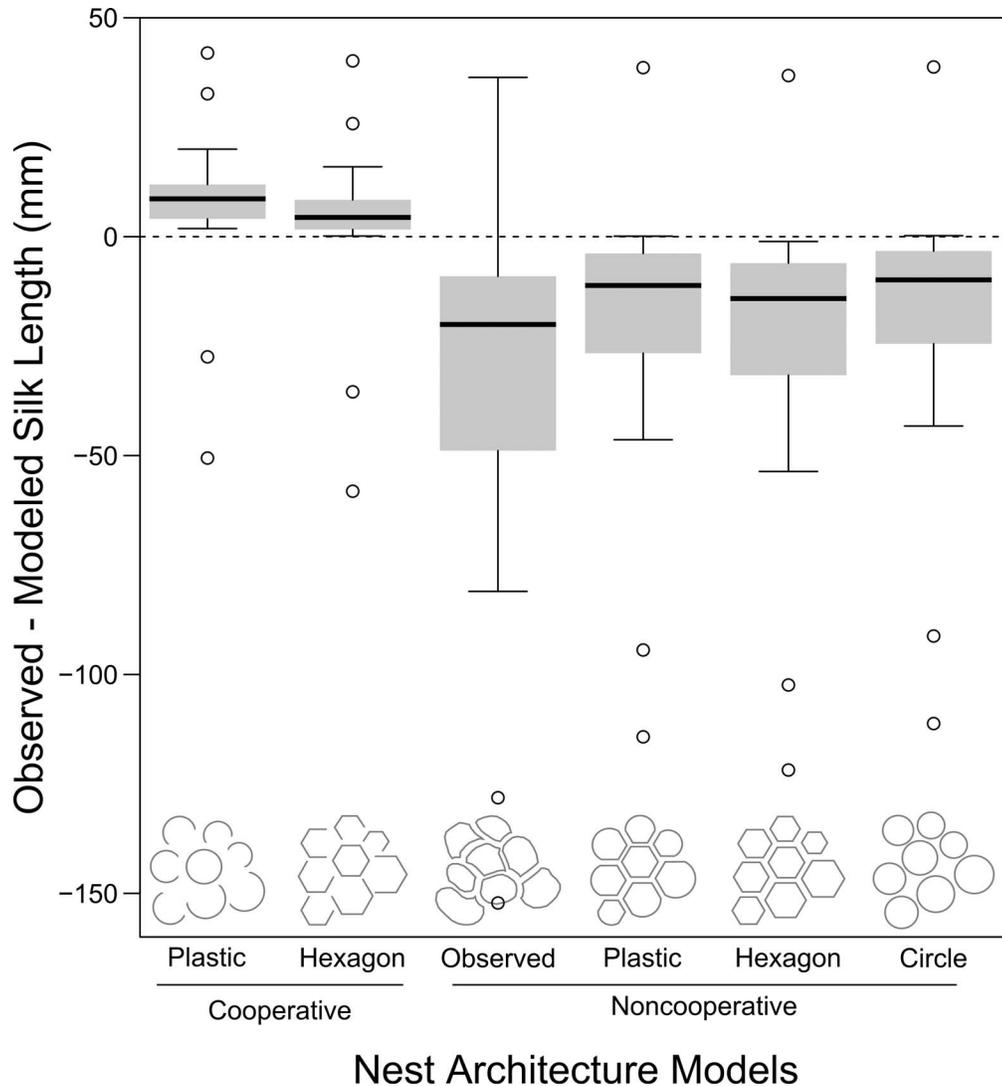
Figure 5.—Box plots comparing observed silk use with five models (Table 2). Observed nest architecture used less silk compared to modeled cooperative and non-cooperative hexagons. All groups are significantly different from each other and from observed nests at $a = 0.05$ by paired, pairwise t-test with Holm's adjustment, except Cooperative Hexagon, which does not differ from the (cooperative) observed nests ($p = 0.185$).

Models using derived perimeters were composed of inflexible perfect circles or regular hexagons, each with an area equal to an observed cell in a real nest. Using inflexible shapes with varying area results in gaps between cells (see model illustrations in Table 2). As such, these models are more conservative estimates of construction costs, since additional building material would be required if all cells connected in the same fashion as natural nests.

For all models, we assumed that groupmates place nest cells in the optimal locations. This being the case, the number of walls available for reuse were geometrically limited to two. However, if groupmates behave non-optimally and build cells utilizing fewer walls than were available, a future cell may be positioned in a location that can reuse three or more already-constructed cell walls, exceeding the two-wall maximum that occurs in our nest models. It remains unclear how closely pseudoscorpions might follow the optimal construction pattern. Future studies using timelapse photography of nest

construction might reveal this and would be an interesting step forward. Nevertheless, we found that observed pseudoscorpion nest architecture rivaled that of honey bees and outperformed all but the cooperative plastic model while remaining flexible enough to adapt to the varying topology of tree bark crevices.

Paratemnoides elongatus nests in this study were composed of 2–17 cells, with an average of six. In situ, nest size appears limited by substrate characteristics. In particular, the exfoliating outer bark (rhytidome) of *P. elloitti* trees includes laminated sheets of tissue divided by a tessellated pattern of fissures (terminology *sensu* Junikka 1995). *Paratemnoids elongatus* build nests only between laminations, such that the floor and roof of the nest are bark, while the walls, only a few mm high, span bark layers. As such, nests cannot be built across bark fissures, having no roof support. Thus, the matrix of bark on a tree appears to limit, at least in part, social group size. That being said, our sampling approach was not intended

to infer the average nest size and was limited to one locality. Variation in nest characteristics across the species range may occur.

Further, variation in cell size within a nest may be important. For example, circle packing algorithms can exceed the packing density of a hexagonal arrangement by packing circles of different size. Since nest cells are made by juveniles of one of three instars, a variety of cell sizes can make up a nest, resulting in higher construction material efficiency than the cooperative plastic model.

Our comparative nest modeling analyses suggest that pseudoscorpions may have evolved social group living and cooperative nest construction by direct fitness effects alone. The benefit of taking advantage of existing construction materials by building a new cell next to a preexisting one directly benefits the new cell builder. However, other benefits of sociality could be at play. While the genetic relationships of social pseudoscorpion groups have never been examined, it seems likely that groups are egalitarian (sensu Bourke 2011), and unrelated to each other, given that several adults are usually found in nests. Individuals acting selfishly to reduce their own silk use can result in cooperative nest construction and provide reproductive benefits. In addition to the shared wall use, this is primarily because nests are reused by offspring and future generations (pers. obs.).

Brach (1979) described *P. elongatus* as, "the most atypical pseudoscorpion", and was the first to describe them as social (Brach 1978). Brach (1979) found "communal silken molting nests" with individuals that exhibited cooperative prey capture and nest construction. Brach (1978) described pseudoscorpion colonies as being composed of five to 50 individuals, with nests of up to 14 cells, with more pseudoscorpions than cells present (Brach 1978). Our findings are consistent with these, as we found nests with up to 17 cells and with many more individuals. We also found that nests tended to occur low or at the base of trees, where moisture from the ground contributed humidity to the microhabitat, consistent with past observations (Brach 1978). Many pseudoscorpions across several families use layers of bark as refuge facultatively or exclusively (Brach 1979). In fact, *Verrucaditha spinosa* (Banks, 1893), *Cheiridium* sp. Menge, 1855, *Garyops depressus* Banks, 1909, *Idiogaryops paludis* (Chamberlin, 1932), *Parachernes latus* (Banks, 1893), *Americhernes longimanus* Muchmore, 1976, *Dendrochernes morosus* (Banks, 1895), and *Parachelifer superbus* Hoff, 1964 are all sympatric and generally syntopic with *P. elongatus* (Brach 1979).

From a game theoretic perspective, this social interaction of pseudoscorpions engaged in nest construction fits a snowdrift or hawk-dove game, where the first individual to construct a cell does not benefit from, but is also required for, cooperative construction (Maynard Smith & Price 1973). In this case, the first individual would not pay a cost compared to solitary construction because the first cell requires silk equivalent to a singular solitary cell. This results in a commensal form of the snowdrift game (Maynard Smith & Price 1973). This opens up the interesting proximate question of whether individuals build a cell first or search for existing nests to join, a dynamic that may shape group sizes and would be fruitful for empirical and theoretical investigation alike. Further, it indicates that group nest construction can occur without direct cooperation

and among selfish actors, as the relationship between co-builders is commensalistic. That being said, it seems likely that commensalistic nest construction could lead to other benefits of sociality, like cooperative prey capture or brood care. Indeed, other species of pseudoscorpion have been documented building moltaria or brood chambers adjoined to another, but otherwise not interacting cooperatively (Vachon 1951; Weygoldt 1965). Nevertheless, nest construction benefits alone could explain collective construction alone, and may serve as a null model to test for other benefits of sociality.

Overall, we found that nests of the social pseudoscorpion *P. elongatus* are highly efficient in design, and that nearly all group members gain direct benefits of cooperative nest construction by reducing the per-capita construction costs for all but the first individual. Nest efficiency best matched models used to describe honey bee hive construction, and further investigation into the benefits of construction plasticity and flexibility is warranted. We show here that group nest construction alone can provide sufficient direct benefits to promote the evolution of sociality, even among individuals acting selfishly.

ACKNOWLEDGMENTS

SUPPLEMENTAL MATERIALS

Available online at https://doi.org/10.1636/JoA-S-21-017.s1

Table S1.—Pairwise comparisons of estimated silk use for pseudoscorpion nest architectures.

Supplemental equations— Mathematical derivations for cooperative and noncooperative model equations used in the study.

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