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When missing legs, *Prionostemma* Opiliones roost more frequently in the aggregation's centers

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Abstract. Many animals form roosting aggregations for defensive benefits, such as early warnings and reduced capture probability. These benefits may vary depending on the individual's location within the aggregation and its phenotypic condition. In the lowland rainforest of Costa Rica, Opiliones of *Prionostemma* Pocock, 1903 (Sclerosomatidae) form daytime roosting aggregations, and leg loss occurs in over half of the individuals. We tested whether the leg condition (intact or missing at least one leg) in one species (*P.* sp.2) affects roosting location within the group by experimentally inducing the formation of aggregations overnight. We found that autotomized individuals (with < eight legs) roosted more frequently (29%) in the center of groups than intact (eight-legged) individuals (20%). This finding suggests that leg loss may influence individuals to select more protected positions within the group. These arachnids might modify their aggregation behavior to compensate for the reduced locomotor performance and potential reduced sensory performance that derives after leg loss. Broadly, our work provides novel experimental data on how variable phenotypic conditions affect the decisions animals make while engaging in group living.

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Many animals engage in group living to obtain defensive benefits, which can vary based on both the aggregation's conditions (size, location, proximity to resources) as well as the needs of aggregating individuals (Guindre-Parker & Rubenstein 2020; Jolles et al. 2020). The benefits animals might obtain when aggregating (e.g., reduced predation risk, earlier warning of potential predators, collective retaliation, or better access to resources or mates) might affect their decision-making process of whether to join an aggregation (Vanthournout et al. 2016; Guindre-Parker & Rubenstein 2020; Escalante et al. 2022). For instance, individuals can decide whether to join an aggregation based on where they can place themselves within said aggregation (Hamilton 1971; Stankowich 2003).

A key question in the study of animal grouping is how benefits vary spatially within the group. The individual risk of being preyed upon varies based on the location within the group relative to the approaching predator, a phenomenon known as the selfish herd (Hamilton 1971; Lehtonen & Jaatinen 2016). Additionally, there is a greater risk of predation on the periphery of a group relative to its center, a phenomenon known as marginal predation (Kruuk 1964; Hamilton 1971; Stankowich 2003; Knotts & Griffen 2016).

Once aggregated, the within-group positioning can be determined by the phenotypic variation of the aggregated individuals (Jolles et al. 2020). For example, in cod (*Gadus morhua*), larger fish usually lead the school (DeBlois & Rose 1996); in pigeons (*Columba livia domestica*), faster birds are the leaders when they move (Pettit et al. 2015); while in zebras (*Equus burchellii*), pregnant and lactating females position themselves at the front of the herd to be the first in finding food (Fischhoff et al. 2007). By contrast, individuals with a morphological condition that can affect their well-being (i.e., individuals with lower aerobic capacity, reduced mobility, or high levels of parasitism) are usually found at the back of groups (Killen et al. 2012; Ward et al. 2018). Consequently, an individual's phenotype can influence its likelihood of surviving predator attack survival, given its position within the aggregation.

Daytime groups of motionless individuals may provide defenses in some species of the understudied arachnid order of Opiliones (Grether et al. 2014a,b; Escalante et al. 2022; Villaseñor-Amador & Escalante 2025). These animals spend the day motionless with up to 200 individuals in close proximity and even overlapping their legs in a given roosting site (Escalante et al. 2022; Villaseñor-Amador & Escalante 2025) (Fig. 1A). Some potential benefits of groups are increased vigilance and a decreased predation risk (reviewed in Escalante et al. 2022). Leg loss is common in these arachnids, and eight species of the sclerosomatid genus *Prionostemma* Pocock, 1903 have populations in which more than half of the individuals are missing at least one leg (Escalante & O'Brien 2024). In seven species of *Prionostemma*, Escalante et al. (2022) found no relationship between roosting solitarily or in groups and their leg condition (intact eight-legged individual or autotomized individuals with fewer than eight legs) (Escalante et al. 2022). However, the specific location within the group where autotomized individuals roost has yet to be studied.

The layout of these arachnids' aggregations suggests potential asymmetric defensive benefits. Aggregations of *Prionostemma* have individuals usually roosting in only one layer—i.e., no animals are on top of each other (Escalante et al. 2022; Villaseñor-Amador & Escalante 2025). This layout creates a two-dimensional arrangement of individuals, suggesting that the aggregations' most protected locations vary based on predator approach angles. Predators of Opiliones include lizards, birds, small mammals, and arthropods (Cokendolpher & Mitov 2007; Silva et al. 2018; Powell et al. 2021), but no study has assessed how they approach Opiliones aggregations. However, if a predator approaches from the edges (i.e., parallel to the layer of individuals), individuals in the center are most protected from a first approach (Suire et al. 2023). In contrast, if a predator approaches from the top (i.e., perpendicular to the 2-dimension layer of individuals), the vulnerability of prey animals will depend on the predators' targeting (Lambert et al. 2021; Jolles et al. 2022). For example, pike (*Esox lucius*) targets prey in its frontal "strike zone", which makes individuals in central locations more likely to be attacked (Jolles et al. 2022), while bass (*Micropterus salmoides*) targets the periphery, even if coming from above the prey group (Romey et al. 2008). This is especially important considering that *Prionostemma* Opiliones have a variety of predators with different targeting strategies: invertebrates like spiders, scorpions and ants, and vertebrates like lizards and birds (Grether & Donaldson 2007; Escalante & Elias 2021; Villaseñor-Amador & Escalante 2025). How interactions between

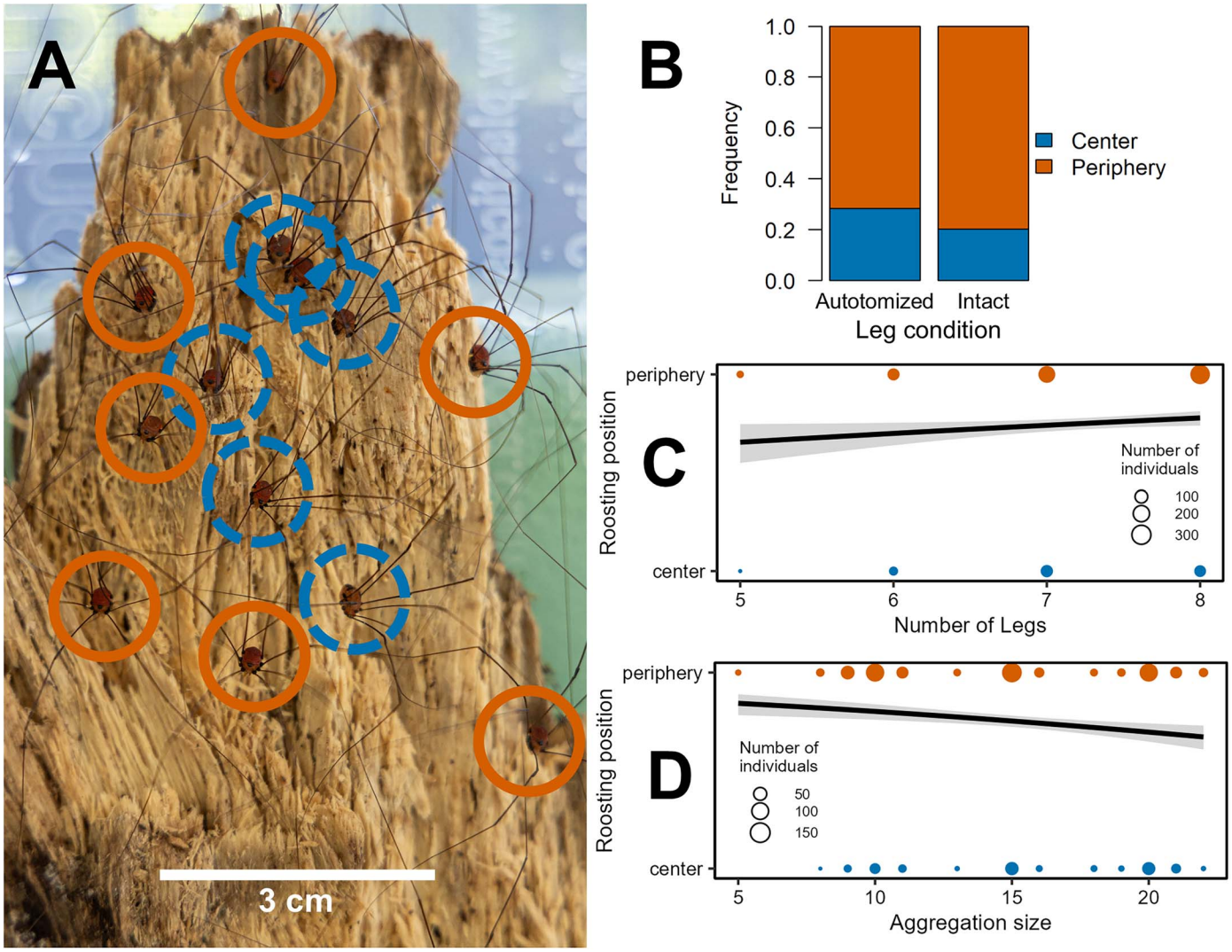


Figure 1.—(A) Roosting location of *Prionostemma* sp.2 Opiliones: center (individuals marked inside dashed blue circles) or periphery (individuals marked inside solid orange circles), at La Selva Research Station, Sarapiquí, Costa Rica. Photo by: StoneFlyCR. The circles in this figure illustrate only the first step of our method for assigning individuals to the categories "central" or "peripheral", as we sorted individuals based on the whole range of visible legs (see Methods for the full description). (B) Frequency of the location of Opiliones in the groups according to their leg condition: fewer than eight legs (autotomized) or with eight legs (intact). Note that eight-legged animals were more common on the periphery than in the center. (C) The likelihood of observing the roosting position (center or periphery) as a function of the number of legs. Points represent the eight possible combinations of the number of legs by roosting position, while the size of the circles reflects the number of individuals observed ($n = 865$). The solid black line and shaded area represent a visual mean estimate predicted by the best-fitted binomial GLM and its 95% confidence interval. (D) The probability of observing the roosting position (center or periphery) given the size of the aggregation. Points represent the observed combinations of roosting position by aggregation size ($n = 25$; the aggregation with five Opiliones did not have any individual in the center), with the size of circles proportional to the number of individuals observed. The solid black line and the shaded area represent a visual mean estimate predicted by the best-fitted binomial GLM and its 95% CI.

individual vulnerability (e.g., due to the negative consequences of leg loss for locomotion [Escalante & O'Brien 2024]) and predator approach affect animal roost locations remains unknown. Ultimately, understanding the influence of body condition on the specific roosting location will inform collective animal decision-making.

We tested the hypothesis that the leg condition of *Prionostemma* Opiliones affects the location inside the group where these arachnids roost. Specifically, we predicted that individuals with fewer than eight legs would roost in the center more often than in the periphery, based on the selfish herd theory and marginal predation concept (Kruuk 1964; Hamilton 1971; Stankowich 2003; Lehtonen & Jaatinen 2016). On the contrary, this pattern would not occur in intact individuals. Since autotomized Opiliones move more slowly than intact Opiliones and might have compromised sensory abilities, as these arachnids have many sensory structures in their legs (reviewed in Escalante & O'Brien 2024), they might seek the group's center. This location could yield a lower probability of being contacted first by potential predators approaching from the edges of the aggregations. This central position could provide an anti-predation buffer and give autotomized Opiliones more time to successfully escape while predators attempt to grab individuals from the periphery.

METHODS

We studied Opiliones of *Prionostemma* sp.2 (following the nomenclature in Proud et al. 2012) (family Sclerosomatidae) at La Selva Research Station, in Puerto Viejo de Sarapiquí, Heredia, Costa Rica (10.4311 N, 84.0068 W, elevation: 50 m) in February 2024. Several species of Sclerosomatidae roost during the daytime (Wade et al. 2011; Escalante et al. 2022; Villaseñor-Amador & Escalante 2025) in groups of the same or multiple species (Escalante et al. 2022) in hollow logs, trees, palm trunks, mossy branches, and large plant leaves like *Heliconia* (Grether & Donaldson 2007; Grether et al. 2014b). At dusk, these arachnids abandon the group and move in solitary to mate and forage (Wade et al. 2011; Proud et al. 2012). Notably, *Prionostemma* species do not aggregate in specific locations that provide any climatic or physiological benefit (Grether & Donaldson 2007; Grether et al. 2014b). We lack knowledge of these Opiliones' behavior while forming the aggregations. It is unknown how individuals in the center get to be in the center. Anecdotal observations by one of us (I.E.) suggest that individuals place themselves next to already roosting individuals. However, it is unknown if individuals "climb" over each other or if there are conflicts—or turnovers—regarding the final location in aggregations.

For lab experiments, we collected individuals on the trails Sendero Tres Ríos (STR) and Sendero Surá (SUR). Throughout 21 days, we collected 865 individuals (405 with eight legs and 460 already missing legs and found with seven or fewer; no autotomy was induced). We conducted this research following research permits of the Costa Rican Government (permit # SINAC-ACC-PI-re-003-2024). Additionally, we ensure the welfare of Opiliones throughout all stages of this work by following suggested guidelines and best practices (ASAB/ABS 2023; Escalante & O'Brien 2024).

To test our hypothesis of the location within the group to roost, we first placed the collected Opiliones in an arena composed of a plastic shoe box (33 × 20 × 12 cm) at night (19:00–21:00 h) to induce the formation of aggregations overnight (i.e., aggregations were formed by the dawn of the following day). Previous work (Villaseñor-Amador & Escalante 2025) suggested the feasibility of this box size. We studied 858 individuals, 46% of whom had eight legs, 38% had seven, 13% had six, and 3% had five (we did not note which legs were missing, i.e., from pairs I, II, III, or IV). We did this in the Environmental Lab at La Selva (an open-window room with ambient temperature). A 20 × 10 cm wooden surface or bark fragment in each box provided a natural substrate on which to aggregate (Fig. 1A). We kept each box vertical to mimic the tree buttress where Opiliones roost (Escalante et al. 2022). We added a small Petri dish with fresh fruit as food and a wetted cotton ball as water supply in each box.

In each trial, we added a total of 5 to 22 individuals. Previous research in La Selva (Calhoun et al. 2025; Villaseñor-Amador & Escalante 2025), has found that 48–53% of Opiliones' field aggregations are of this size. This experiment was part of a broader project (Villaseñor-Amador & Escalante 2025) testing the effect of group size on behavioral responses such as bobbing—which were recorded the following morning after recording each individual's position on the aggregation (see below). Consequently, we studied 32 small groups (5–11 individuals, $n = 308$), 17 medium groups (13–16 individuals, $n = 255$), and 15 large groups (18–22 individuals, $n = 304$). For each trial, we had similar numbers of individuals with both leg conditions: the ratio of autotomized to intact individuals across the 64 groups we studied was 1.17:1.

We report the proportions of autotomized and intact Opiliones in an aggregation's center and periphery, which allowed us to make inferences while also controlling for the variation in group sizes. The morning after placing individuals in the arenas, we photographed each group with a GoPro Hero 8 (GoPro, Inc., San Mateo, CA, USA) placed 50 cm away. To identify individuals as in the "center" or the "periphery" of the group from the pictures, we drew circles centered on their bodies. Then we scaled up the circles to encompass the full span of their visible legs: any individual whose circle formed part of the group's boundary was assigned to the periphery, while all the others were classified as part of the center (Fig. 1A).

To test if leg condition and group size affect the roosting location choice, we ran a generalized linear model with binomial distribution with group position (center or periphery) as the binomial response variable, number of legs (5, 6, 7, or 8) and group size (5 – 22 individuals) as numerical continuous explanatory variables. For this model, we included data for 865 individuals in 64 aggregations. We performed all analyses in R version 4.2.1 (R Core Team 2022), used the *glm* function to run the model, and the *ggplot2* package (Wickham 2016) to plot the binomial regressions.

RESULTS

We found that autotomized individuals (< eight legs) roosted more frequently (134/460 individuals; 29%) in the center of groups than intact (eight-legged) individuals (82/405; 20%) (Fig. 1B). This was supported by a positive effect of the number of legs on the likelihood of observing Opiliones in the periphery of the aggregation (estimate ± SE = 0.22 ± 0.1; $P = 0.026$; Fig. 1C).

We also found that larger groups had more individuals in the center. This was supported by a negative effect of group size on the likelihood of observing an individual in the periphery (−0.06 ± 0.02; $P = 0.001$; Fig. 1D). It is worth noting that—given the groups' two-dimensional structure (Fig. 1A)—most (75%) of the Opiliones were roosting in the periphery.

DISCUSSION

We experimentally demonstrated that the proportion of Opiliones roosting in the center versus the periphery of an aggregation varies based on their number of legs. Autotomized Opiliones roosted more frequently in the aggregations' center than intact individuals, supporting our hypothesis that their leg condition affects the location inside the group to roost. These novel findings demonstrate that the variation in the morphological state of individuals contributes to their decision-making of which specific location to roost within a group.

Autotomized Opiliones may rely more on collective grouping behavior to protect themselves than intact individuals. In the center locations, they could be less likely to be attacked, as predicted by the selfish herd and the marginal predation theory (Kruuk 1964; Hamilton 1971; Stankowich 2003; Lehtonen & Jaatinen 2016). On the one hand, larger aggregations can amplify this potential benefit, as we found that Opiliones roosted more in center locations the larger the aggregation was. Roosting surrounded by more individuals can increase the chances that autotomized individuals survive a predator attack. On the other hand, small aggregations

might not have enough individuals to have enough center locations for automatized Opiliones to roost. Since all aggregations in our experiment had a similar-sized bark piece for roosting, larger groups had more individuals occupying the same area, creating more center positions. In contrast, smaller groups had fewer individuals, limiting the number of fully surrounded center locations. Regardless of aggregation size, we currently lack information on whether individuals in the center of aggregations experience fewer predation attempts than in the periphery. Additionally, because faulty molts can result in autotomy (Escalante & Elias 2021; Escalante & O'Brien 2024), autotomized Opiliones' location in the center of aggregations may reflect their age (i.e., individuals with longer lifespans have experienced more molts and consequently a higher chance of losing legs), rather than a defensive behavioral response. Future experimental work can test this possibility.

Because autotomized Opiliones move slower than intact ones and might have compromised sensory abilities (Guffey 1999; Domínguez et al. 2016; Escalante et al. 2020; Escalante & Elias 2021), they could roost in center positions to receive alarm signals faster and escape. Opiliones of another family use volatile chemical signals to alert the presence of potential predators (Machado et al. 2002). This possibility will work for agonistic stimuli coming from the group's periphery, such as a predator approaching from the edges of the group. However, our hypothesis has the caveat that if predators approach from the top of the single-layer *Prionostemma* aggregation, the location categories we used (center versus periphery) might not provide differential benefits. Regardless of the position of the Opiliones within the aggregation, the survival of the individual may ultimately depend entirely on the predators' targeting selection (Romey et al. 2008; Jolles et al. 2022). Additionally, a predator approaching from the top might trigger different responses in aggregated Opiliones or different survivorship success. These issues should be addressed in future research.

Understanding which animals prey on these Opiliones and how they approach them will be crucial to support our findings fully. Predators of Opiliones are diverse and include lizards, birds, small mammals, and arthropods (Cokendolpher & Mitov 2007; Silva et al. 2018; Powell et al. 2021). Though no study has evaluated predation on *Prionostemma*, anecdotal observations report predation events by wolf spiders (Escalante & Elias 2021), scorpions, ants, a lizard (Grether & Donaldson 2007), a Golden Silk Orb-weaver spider (*Trichonephila clavipes* (Linnaeus, 1767)), and a Wedge-billed Woodcreeper (*Glyphorynchus spirurus*) (Villaseñor-Amador & Escalante 2025). These animals that likely hunt *Prionostemma* vary in their lifestyle (diurnal *vs*. nocturnal) and the cues they use to find prey (sight, proprioception). However, those predators (except the orb-weaver) will likely approach an Opiliones aggregation coming from the aggregation's edges. If this scenario accounts for most predation attempts, then center locations will be more beneficial for *Prionostemma* Opiliones in surviving predator encounters.

Animals can modify their behavior to compensate for the potential increased exposure to predators driven by variation in their morphological condition, potentially leading to using more protected within-group locations (Hamilton 1971; Martin & Salvador 1992; Stoks 1999). By changing how they place themselves in a given position within the aggregation, Opiliones can compensate for the adverse effects of leg loss, including the effects on locomotion, sensory capabilities, and habitat use (reviewed in Escalante & O'Brien 2024). A potential compensation for leg loss was experimentally demonstrated in how *Prionostemma* sp.5 uses specific microhabitats (Escalante & Elias 2021) and how *P*. sp.2 uses different moving gaits (Escalante et al. 2020). Furthermore, to understand how morphological variations can impact decision-making and compensatory behaviors, future work can quantify the response to predator cues and alarm signals of Opiliones—and many other taxa—with variable leg conditions roosting in different locations within an aggregation.

In summary, our results show that morphological variation, specifically leg autotomy, influences the grouping behavior of Opiliones within aggregations. Autotomized individuals were more likely to be in central positions, possibly as a strategy to reduce predation, compensating for their reduced mobility and sensory capabilities. This behavior fits within the framework of well-established theories like the selfish herd and marginal predation theory while raising new questions about the relationship between spatial positioning and survival. Future studies can evaluate the within-group positioning effect of predator approach and alarm signaling.

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DATA AVAILABILITY

The complete dataset and code are publicly available on the DRYAD repository [https://doi.org/10.5061/dryad.zw3r228j5].

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