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SHORT COMMUNICATION

Ecological Entomology

Trophic egg provisioning in spiders: Repeated evolution predicted by body size and climatic zone

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Abstract

1. Trophic egg provisioning, the production of unfertilized eggs that serve as food for offspring, represents an intriguing form of maternal investment that enhances offspring fitness; yet its evolutionary drivers across invertebrates remain poorly understood. In spiders, this strategy is sporadically documented, but its evolution remains virtually unexplored.
2. We compiled data on 39 spider species from 26 genera and 14 families representing, to our knowledge, all spider species with confirmed trophic egg provisioning records in the published literature.
3. We demonstrate that trophic egg provisioning has evolved independently multiple times across distantly related lineages, with no significant phylogenetic signal, suggesting that its evolution may be associated with shared selective pressures. By examining ecological and phenotypic factors across spiders, we found that female body length showed a strong positive association with trophic egg provisioning, indicating that larger females possess greater capacity for resource allocation to extended maternal investment. The prevalence of trophic egg provisioning was significantly higher in non-tropical regions than in tropical ones, suggesting that environmental variability in temperate zones favours this behaviour as a buffer against unpredictable resource availability.
4. Our findings reveal that the evolution of trophic egg provisioning in spiders is shaped by the interplay of morphological capacity and environmental pressure, providing a tripartite explanatory framework for understanding the convergence of extended parental care strategies across phylogenetically distant lineages.

KEYWORDS
body size, maternal investment, phylogenetic signal, spiders, trophic egg provisioning

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INTRODUCTION

Remarkably diverse patterns of parental care are known across animals (Fernandez-Duque et al., 2009). Among them, food provisioning is well known to enhance offspring fitness and survival (Mailho-Fontana et al., 2024). Food provisioning may involve nutritional secretions from parent to offspring, such as milk and milk-like substances, or trophic eggs, all of which contribute to offspring growth (Chen et al., 2018; Mailho-Fontana et al., 2024). These provisioning strategies are often linked to lineage diversification, suggesting a role in shaping evolutionary radiations or being shaped by ecological feedback (Fernandez-Duque et al., 2009). Nutritional secretion is well known and broadly documented across vertebrates, examples being milk substances in mammals and trophic eggs in frogs (Fischer et al., 2019). Among invertebrate lineages, however, the prevalence and evolutionary patterns of nutritional secretion are poorly understood and yet to be extensively investigated.

Trophic egg provisioning is a form of parental care in which mothers produce unfertilized or non-viable eggs that serve as a nutritional resource for their offspring. Among invertebrates, this strategy is perhaps best documented in spiders (Yip & Rayor, 2014). Although parental care has evolved independently multiple times across the spider phylogeny, post-hatching trophic egg provisioning appears to be relatively rare, having been reported only in a few distantly related families, including Amaurobiidae, Agelenidae and Thomisidae (Kim & Roland, 2000). The trophic egg provisioning strategy suggests strong selective pressures favouring extended maternal investment under particular ecological or physiological conditions (Kim & Roland, 2000). For instance, in habitats with fluctuating resource availability, trophic eggs may buffer offspring against starvation during early development (Yip & Rayor, 2014). Despite its potential adaptive significance, the phylogenetic patterns and ecological drivers underlying the evolution of trophic egg provisioning in spiders remain largely unexplored.

Through an exhaustive literature review, we have compiled data on 39 spider species across 26 genera and 14 families documented to exhibit trophic egg provisioning. To our knowledge, this compilation represents the complete set of published records for this trait in spiders. The repeated occurrence of this strategy across phylogenetically diverse lineages suggests it has evolved convergently under specific ecological or life-history contexts. We hypothesize that trophic egg provisioning in spiders has evolved as an adaptive maternal investment strategy in response to key ecological and behavioural drivers, such as body size, climatic zone and habitat status, which are predicted to shape the evolution of this behaviour by mediating maternal investment capacity and resource availability for offspring. By examining ecological and phenotypic factors across a broad phylogenetic spectrum, our study aims to gain insights into the ecological correlates and macroevolutionary patterns that have shaped the distribution of trophic egg provisioning in spiders.

MATERIALS AND METHODS

Using the most comprehensive published spider phylogeny (1362 species, 131 of 132 families; Kulkarni et al., 2023), we quantified phylogenetic signal for trophic egg provisioning (39 species coded as 1; all others 0) using the D-statistic (caper package, 1000 permutations). Ecological and behavioural data for the 39 species were compiled from the World Spider Trait database, including female body length, climatic zone (tropical vs. non-tropical), habitat status, foraging strategy and circadian activity. To account for phylogenetic non-independence, we used phylogenetic generalized linear mixed models (MCMCglmm) with a binomial error structure, including the phylogenetic variance–covariance matrix as a random effect and weakly informative priors. To assess robustness, we repeated the analysis 1000 times, each time sampling 39 non-trophic egg species with probabilities proportional to genus-level diversity, and averaged the estimates. We also reconstructed ancestral states of trophic egg provisioning and climatic zone (castor, ER model, root prior = absence) and female body size (phytools) (see more information in the Supplementary Materials and Methods).

RESULTS AND DISCUSSION

Species with trophic egg provisioning are distributed across several major clades, including the RTA clade (e.g., Lycosidae, Salticidae, Agelenidae and Amaurobiidae), the Orbiculariae (Theridiidae) and other lineages such as Scytodidae (Figure 1). This mosaic phylogenetic pattern suggests that the behaviour is not a synapomorphy of any large spider lineage. To quantify this pattern, we estimated phylogenetic signal for the trait, finding that the observed D value (0.967) did not differ significantly from random expectation ($D = 1$, $p = 0.447$) (marginal $R^2 = 0.011$ and conditional $R^2 = 0.96$), indicating no significant phylogenetic signal. These results demonstrate that trophic egg provisioning is a convergent trait that has evolved independently multiple times across distantly related spider families. The lack of significant phylogenetic signal indicates no strong phylogenetic clustering of the trait.

The bootstrapped phylogenetic generalized mixed models showed that only a subset of predictors was significantly associated with trophic egg provisioning, with climatic zone and body size being the most influential (Figure 2). Female body length (odds ratio = 4.74, $p = 0.002$) showed the strongest positive relationships, while the odds of trophic egg provisioning were lower in tropical than in temperate climatic zones (odds ratio = 0.42, $p = 0.02$; Figure 2), indicating that species from non-tropical (i.e., temperate) regions exhibited higher prevalence. However, it is noteworthy that among the 39 documented trophic egg species, 12 were recorded from tropical regions, demonstrating that while statistically more frequent in temperate zones, this strategy is not exclusive to any single climatic regime. For biological interpretation, a 1 mm increase in female body length corresponds to a 374% increase in the odds of trophic egg provisioning (OR = 4.74). These results indicated that larger females and spiders from temperate regions exhibit a higher prevalence of trophic egg provisioning. In contrast, the habitat status, foraging strategy and circadian activity had no significant effects on the trophic egg provisioning (Figure 2).

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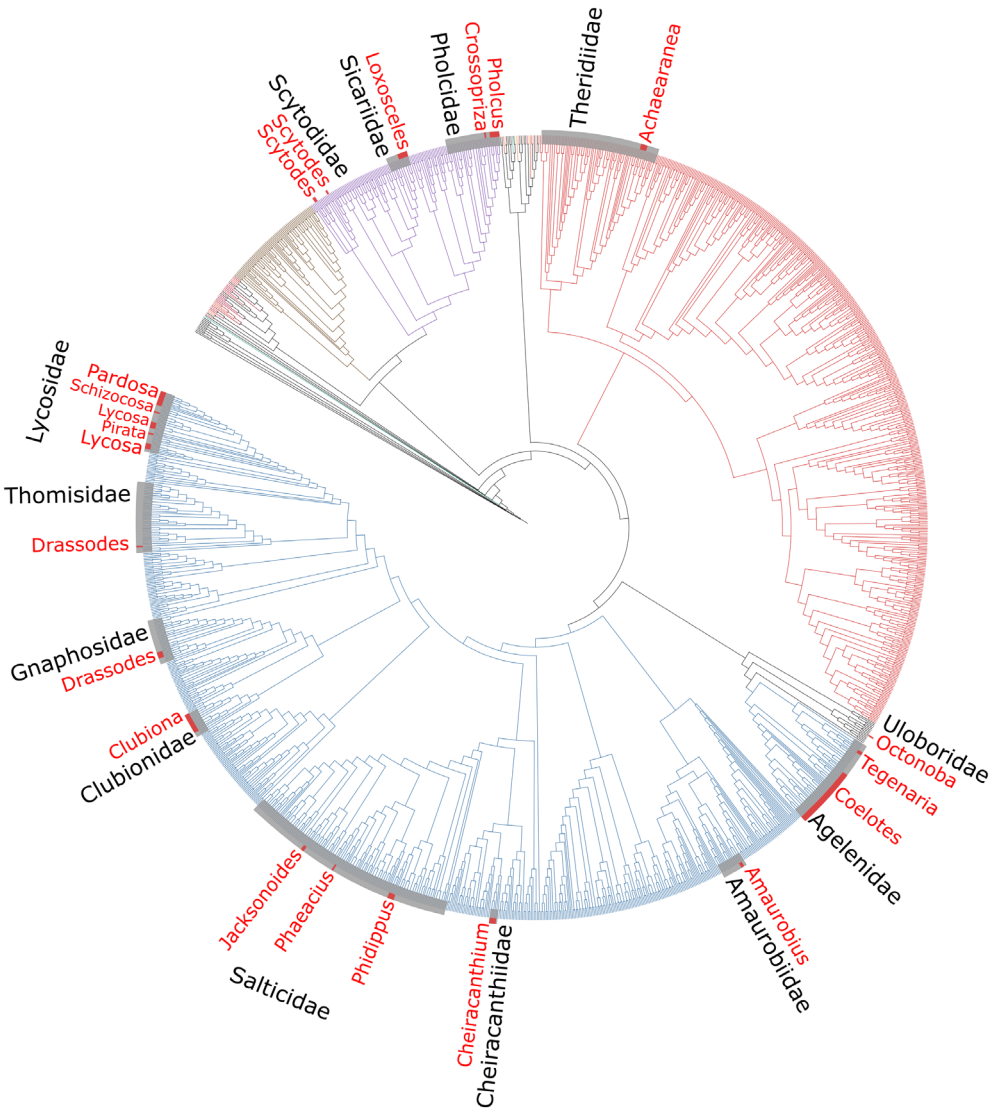

FIGURE 1 Phylogenetic distribution of trophic egg provisioning across spiders. Red labels indicate spider genera that exhibit trophic egg provisioning. The phylogenetic relationships were reconstructed based on the published phylogeny of spiders (Kulkarni et al., 2023). Branch colours represent lineages: Blue = RTA, red = Araneoidea, purple = Synspermiata and brown = Mygalomorphae.

To address potential causality, we reconstructed the ancestral states of trophic egg provisioning, female body size and climatic zone. Trophic eggs originated independently at least 13 times (supplementary Figure S1); at these origin nodes, mean ancestral female body size (7.53 mm) did not differ significantly from the overall mean (8.06 mm; $t = -1.405$, $df = 12$, $p = 0.186$), indicating that body size enlargement did not precede or accompany the origin of this behaviour. In contrast, 10 of 13 origins (76.9%) were reconstructed as temperate rather than tropical, reinforcing the association with temperate environments. These results suggest that climatic factors may have played a more direct role in the initial evolution of trophic egg provisioning, whereas body size capacity likely facilitates its expression or maintenance rather than its origin.

The positive relationship between female body length and trophic egg provisioning aligns with the physiological constraint hypothesis, which predicts that larger females possess greater resource allocation capacity (Yip & Rayor, 2014). In spiders, increased body size correlates with higher fecundity and enhanced energy reserves, enabling investment in additional nutritional eggs without compromising the viability of the reproductive clutch (Kim & Roland, 2000). This increased capacity for investment likely facilitates the evolution of this extended parental care strategy. Our finding is in line with studies in insects exhibiting trophic egg production, where larger female body size is similarly linked to enhanced maternal investment capabilities (Gilbert & Manica, 2010).

Although the tropical association is intriguing, it warrants cautious interpretation. Tropical spiders experience stable conditions that may relax selection for extensive provisioning, whereas temperate spiders face greater variability, potentially favouring trophic eggs as a buffer against nutritional stress (Noriyuki et al., 2012; Perry & Roitberg, 2006; Yip & Rayor, 2014). However, the occurrence of trophic eggs in 12 tropical species indicates that this behaviour can also

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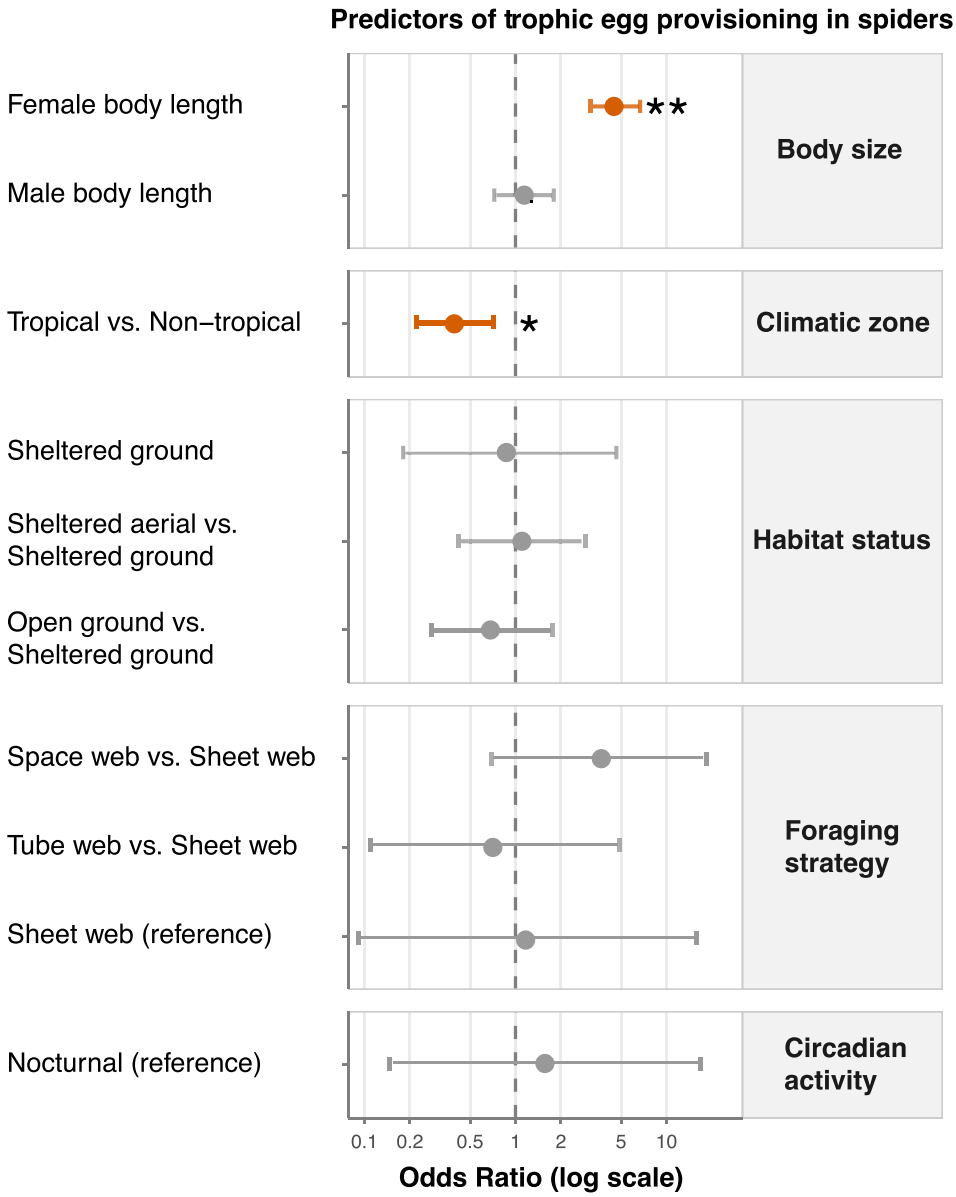

FIGURE 2 Predictors of trophic egg provisioning in spiders. Forest plot showing odds ratios (ORs) and 95% confidence intervals from phylogenetic generalized mixed models. Orange points denote predictors with statistically significant associations ($p < 0.05$), and asterisks mark the same significant predictors; grey points indicate non-significant effects. Horizontal bars represent 95% CIs; the dashed vertical line at OR = 1 denotes no effect. Points to the right of the dashed line indicate positive associations; points to the left indicate negative associations.

arise under stable climates, suggesting that body size capacity, rather than climate alone, may be the primary factor. Observational bias is possible because intensive fieldwork in tropical rainforests has been scarce, but since trophic eggs are typically found in egg sacs or nests, this bias may be limited. Targeted field surveys in under-sampled tropical regions are needed to determine whether the climatic pattern reflects genuine ecological constraints or sampling artefacts. Trophic egg provisioning in spiders represents a compelling example of how behavioural innovation emerges from the intersection of morphological capability (female body size) and environmental pressure (climatic zone). This tripartite explanatory framework advances our understanding of maternal investment evolution and highlights spiders as an exceptional model system for studying the adaptive significance of extended parental care in invertebrates.

Limitation

Trophic egg provisioning may have been underreported and could be more taxonomically widespread than currently documented, and such a sampling bias could influence our evolutionary analyses, which identify female body size and temperate zone occurrence as important factors. Although our bootstrapped sampling procedure provides strong support for the statistical robustness of these associations against random sampling bias, the total number of known trophic egg species remains modest, limiting statistical power to detect subtle interacting effects or to definitively exclude rare alternative drivers. Our ecological and evolutionary interpretations should therefore be considered preliminary and reassessed as more comprehensive natural history data become available; we advocate continued documentation to expand this dataset.

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Our data are mainly species-level presence/absence records without systematic intraspecific data, and female body length was fitted only as a continuous linear term; we therefore cannot distinguish a body size threshold from a linear increase. Future studies should monitor the intraspecific frequency of trophic egg production together with female body size so that threshold or nonlinear models can test how within-species body size variation shapes this trait.

AUTHOR CONTRIBUTIONS

Jiayin Zheng: Methodology; data curation; formal analysis; validation; writing – review and editing; writing – original draft. **Matjaž Kuntner:** Methodology; data curation; formal analysis; writing – original draft; writing – review and editing. **Shuang Xing:** Conceptualization; formal analysis; writing – review and editing; writing – original draft. **Wenda Cheng:** Conceptualization; writing – original draft; writing – review and editing. **Yuanyuan Meng:** Conceptualization; writing – original draft; writing – review and editing. **Shengjie Liu:** Conceptualization; methodology; data curation; investigation; validation; formal analysis; supervision; funding acquisition; visualization; writing – review and editing; writing – original draft.

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CONFLICT OF INTEREST STATEMENT

The authors declare no competing interests.

DATA AVAILABILITY STATEMENT

Data available from Figshare 10.6084/m9.figshare.34841508 (Zheng et al., 2026).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

DATA S1. Supporting Information.

FIGURE S1. Distribution of trophic eggs and their independent origins across the spider phylogeny. Red tips indicate species with recorded trophic eggs (matched at the genus level). Yellow circles mark the 13 independent origin nodes (transitions from state 0 to state 1) as implied by maximum likelihood. Trophic egg behaviour has evolved at least 13 times independently.

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