



Social transitions in sponge-dwelling snapping shrimp

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Sociality is exceedingly rare in the marine environment, with true eusociality found only within a single genus of sponge-dwelling snapping shrimp. This genus is socially diverse and exhibits multiple independent evolutionary origins of both eusociality and communal breeding from pair-forming ancestors. Ecology was critical to the evolution of shrimp sociality, as the transition from host specialization to generalism preceded the evolution of eusociality, and the transition from small to large host sponges favored the evolution of communal breeding. Moreover, a change in life history from planktonic to non-dispersing, crawling larvae only occurred in eusocial species. Here, we present a hypothesis describing the evolutionary transitions toward sociality in shrimp that serves to illustrate how ecology and life history interact to shape social evolution more broadly.

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Introduction

Sociality in the form of cooperative group living is widespread among animals [1[•]], occurring not just in insects [2,3] but also in many other invertebrates and vertebrates [4]. Eusociality, first coined by Batra [5], has historically been defined by cooperative offspring care, overlapping generations, and a reproductive division of labor [2] to encompass caste-based social organizations found in many lineages of Hymenoptera, termites, and some lineages of ambrosia beetles, gall-forming aphids, and thrips [4]. Ants, higher termites, and many social Hymenoptera have permanent morphologically differentiated queen-worker castes, whereas most other eusocial taxa do not [6]. Communal breeding, defined by cohabiting females that share a domicile but build, provision, and breed on their own [7], is common in many lineages of bees, wasps, beetles, and other insects, though this form

of sociality is generally not well documented [3]. Determining the transitions from solitary living to these two forms of social organization is important for understanding how animal sociality has evolved. Yet, transitions to eusociality are typically rare, as illustrated by the corbiculate bees where within the more than 1000 species, the behavior evolved only twice [8]. Additionally, communal breeding generally occurs in clades that lack eusocial species [3], making it challenging to study simultaneously both types of social transitions. Thus, the opportunity to study social transitions within insects is limited to a few lineages, making it important to also examine evolutionary transitions within other non-insect lineages that are socially diverse.

Cooperative group living is almost exclusively a terrestrial phenomenon among arthropods, having evolved only once in the marine environment within a single genus (*Synalpheus*) of sponge-dwelling snapping shrimp. Despite its rarity in the ocean, eusociality evolved independently at least four times within the approximately 45 *Synalpheus* species in the West Atlantic ‘*gambarelloides* group’ of snapping shrimp [9,10^{••}], and likely one or more times in the Pacific *Synalpheus* [11[•]]. *Synalpheus* exhibits three types of social organization that have distinct demographic characteristics, including-specific combinations of colony size and the number of breeding females per colony [10^{••}] (Figure 1). Pair-forming species live in sponges that typically contain only a single breeding pair [11[•]]. This is the ancestral social state shared by most other alpheid snapping shrimp [12]. Communal species live in groups of multiple unrelated breeding pairs [11[•]] with roughly equal ratios of adult males and females [13], but their social behaviors are not well characterized. In contrast, eusocial species typically contain a single ‘queen’ or at most a few queens and up to several hundred non-breeding but totipotent ‘workers’ [14] that are likely to be siblings and the offspring of the queen [15]. Workers defend their host sponges against any foreign intruders and, in some species, show signs of behavioral and morphological differentiation [15–18].

Social sponge-dwelling snapping shrimp exhibit a ‘fortress defense’ social syndrome, where social species live in or near their food and have mobile offspring that require little or no provisioning [19]. Despite the fortress defense social syndrome being found in diverse animal lineages (e.g. aphids, thrips, polyembryonic wasps, wood-dwelling termites, and naked mole-rats [1[•],19,20]), the evolutionary transition toward eusociality is less well studied among fortress defenders than in central place foragers like the Hymenoptera and higher termites.

Moreover, communal breeding has also evolved multiple times from pair-forming species within *Synalpheus* [10**], although the exact number of transitions is unclear because some pair-forming species occasionally form communal groups [10**,11*]. Thus, sponge-dwelling snapping shrimps provide a unique opportunity to study the evolutionary transitions toward two very different forms of social organization within a single, relatively recently evolved genus [21]. Here, we review studies on the evolutionary transitions toward eusociality and communal breeding in *Synalpheus*, illustrating how different forms of social behavior evolved in relation to ecology and life history. Furthermore, we develop a hypothesis that describes the evolutionary transitions toward sociality in *Synalpheus* shrimp that may serve to illustrate how ecology and life history interact to shape social evolution more generally in arthropods.

Evolutionary transitions toward sociality

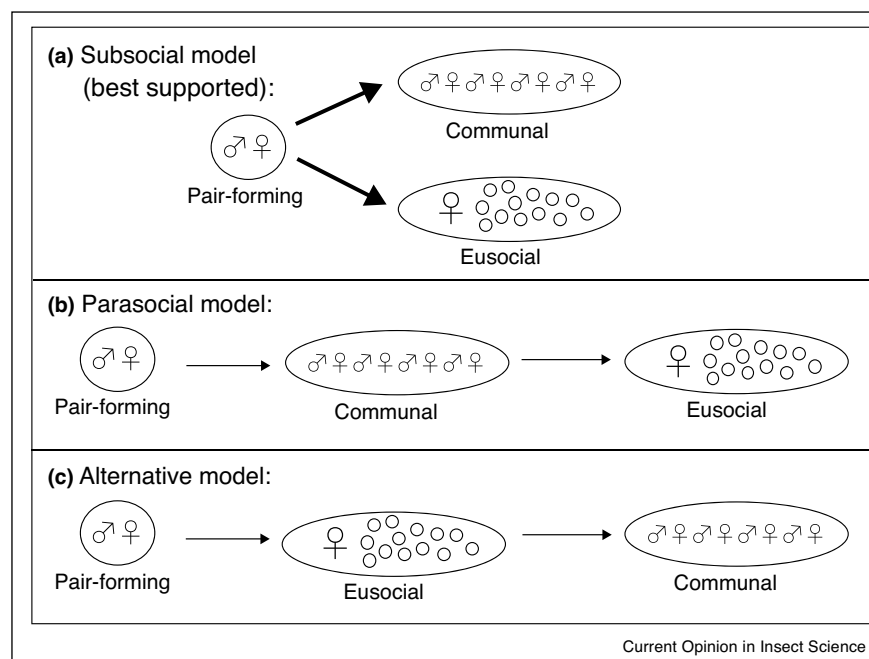
Two alternative models of social evolution have been proposed to explain the evolutionary transition to eusociality from a non-social ancestor. The ‘subsocial model’ suggests that eusocial species evolved from an intermediate ancestor whose immature offspring remained in the parental nest under the mother’s care, forming an aggregation of related individuals that did not interbreed [22,23]. Alternatively, the ‘parasocial model’ [22] suggests

that eusocial species evolved from an intermediate ancestor where unrelated breeders of the same generation aggregated to form ‘communal groups’ characterized by low reproductive skew. In essence, the two models disagree on whether or not eusocial societies passed through a low-skew, intermediate form of social organization (e.g. communal breeding) during their evolution (Figure 1). *Synalpheus* shrimp provide an opportunity to test between the subsocial and parasocial models of social evolution because of the social diversity within the genus and the multiple independent evolutionary origins of eusociality [21,24]. Evolutionary transition modeling suggested that communal and eusocial shrimp species are alternative endpoints that evolved directly and independently from pair-forming species along different pathways [10**] (Figures 1 and 2). Thus, eusociality in shrimp appears to have arisen via the subsocial model, a finding that reaffirms the generality of the subsocial evolution of sociality initiated by the formation of closely related family groups, as observed among both invertebrates and vertebrates [23,25–27].

The role of ecology in social transition

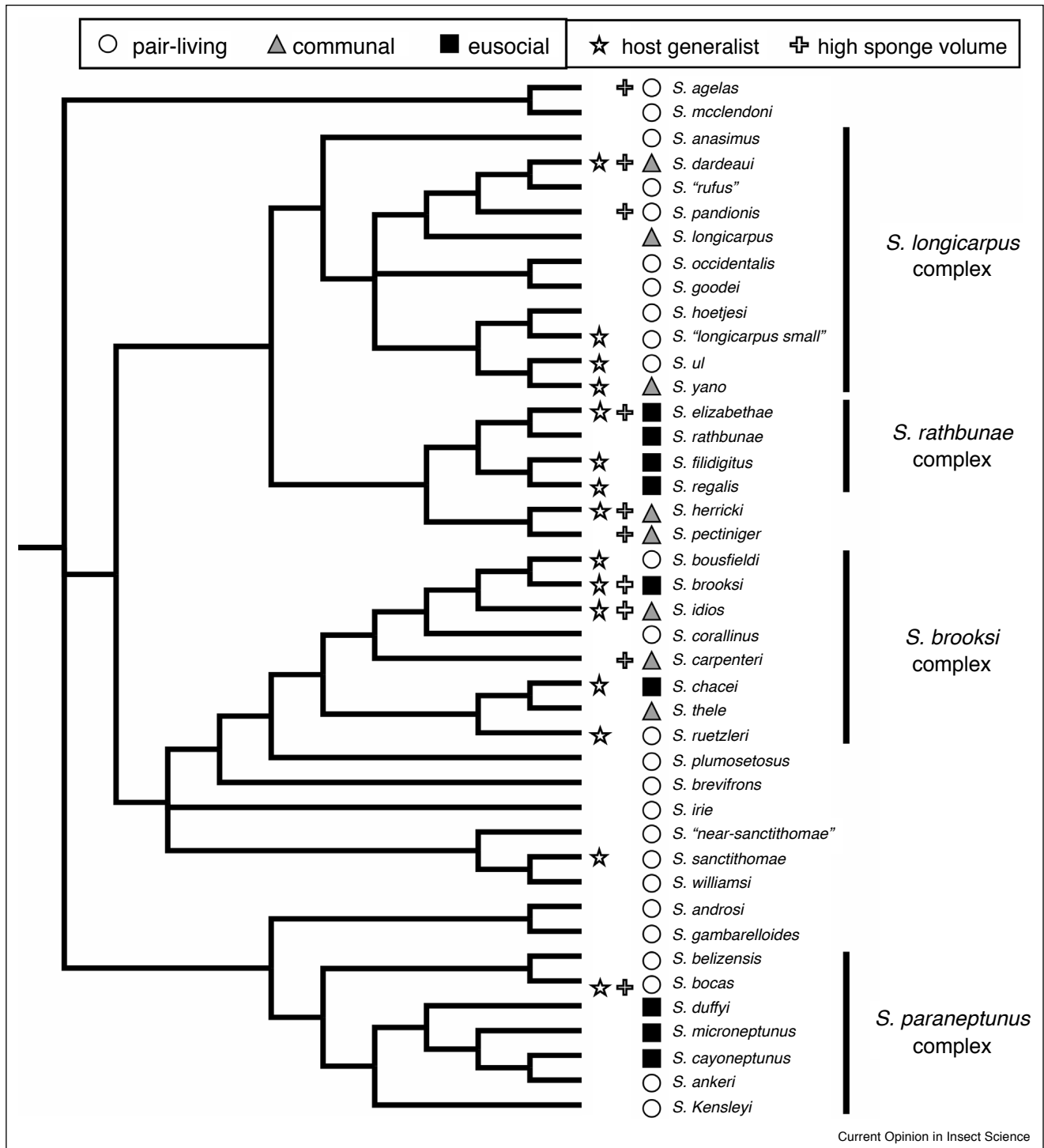
All *Synalpheus* shrimp species are obligate sponge-dwellers that spend their entire adult lifecycle inside the canals of marine sponges. Each shrimp species utilizes a specific set of sponges among about 20 habitable species [28**].

Figure 1



Three models of social transition among pair-forming, communal, and eusocial *Synalpheus* species. The subsocial and parasocial models (a and b) disagree on whether or not eusocial species passed through a communal stage during their evolution. Additionally, communal species could represent a secondary loss of eusociality (c). In sponge-dwelling snapping shrimp, the subsocial model is best supported and suggests that eusociality evolved from a pair-forming state without a transition to communal breeding [10**]. Male and female symbols indicate reproductive individuals, whereas circles indicate non-reproductive workers of either sex in a eusocial colony.

Figure 2



Summary of published social and ecological traits on the latest *Synalpheus* phylogeny. The tree depicts a Bayesian phylogeny of sponge-dwelling snapping shrimp in the West Atlantic gambarelloides group based on COI, 16S, and EF2 and 33 morphological characters (after [43]). Social organizations were classified according to demographic characteristic of colonies (i.e. all conspecific individuals that occurred in a single sponge) [10**,11]. Specifically, species with small colony sizes (<8 individuals) are considered pair-forming (all of them have a modal colony size of two individuals), species with both larger colony sizes (≥8 individuals) and many ovigerous females (≥3) are considered communal, and species with large colony sizes (≥8 individuals) but few ovigerous females (<3) are considered eusocial. Sponge host specificity and sponge host volume were taken from [28**]. Specifically, host generalist species have >2 sponge hosts and specialist have ≤2 sponge hosts. Host sponges were split into high and low volume at the second tertile (66.6% quantile; 385.18 mL).

The shrimp-sponge association is likely to be mutualistic: shrimp gain shelter and obtain food from sponges, which in turn are protected from predators by the aggressive defense behavior of the shrimp [29,30]. More than 20 years of field surveys has shown that unoccupied sponges are almost always absent in the field [15,31,32], suggesting that habitat saturation is likely to be a key ecological pressure in sponge-dwelling shrimp, both social and non-social species alike.

Just as the competitive superiority of organized groups may have facilitated the ecological dominance of social insects like ants [33], sociality in *Synalpheus* may confer an ecological advantage by enhancing their ability to acquire and defend the limited host sponges. Consistent with this hypothesis, eusocial *Synalpheus* species in Belize were more abundant, occupied more sponges, and had a broader host breadth than pair-forming and communal species [9]. Although communal species are not as ecologically dominant as eusocial species, communal species appear to have higher population stability than eusocial species because local extinction of eusocial, but not communal, species has been observed in multiple regions of the Caribbean [34]. These observations suggest that communal species may be demographically more stable than eusocial species, despite the ecological dominance of eusocial species.

The wider sponge host breadth in eusocial *Synalpheus* species means that eusocial species tend to be niche generalists, a pattern that could be explained by two competing hypotheses relating sociality to ecology. First, cooperation may have allowed eusocial species to expand their ecological niches and become sponge host generalists (social conquest hypothesis) [35,36]. Alternatively, host generalist species may have experienced stronger ecological constraints due to competition, which in turn promoted the evolution of cooperation (social transition hypothesis). In *Synalpheus*, both host generalism (having a wide breadth of sponge hosts) and occupation of larger sponges appear to precede the transitions to eusociality and communal breeding [28**] (Figure 2). Consistent with the social transition hypothesis and the idea that ecological generalism facilitates the evolution of eusociality, transitions to eusociality occurred almost exclusively in lineages that were already host generalists. In contrast, the transition toward communal breeding occurred almost exclusively in lineages that live in sponges with large volumes. Therefore, different ecological factors appear to have influenced the independent evolutionary origins of sociality in *Synalpheus* shrimp. Moreover, while the ecological success of ants suggests that advanced sociality allows for niche expansion [33], a phenomenon also observed in terrestrial groups including birds and burying beetles [35,36], this does not seem to be the case in *Synalpheus*, in which ecological generalism facilitates the evolution of sociality. Ultimately, these

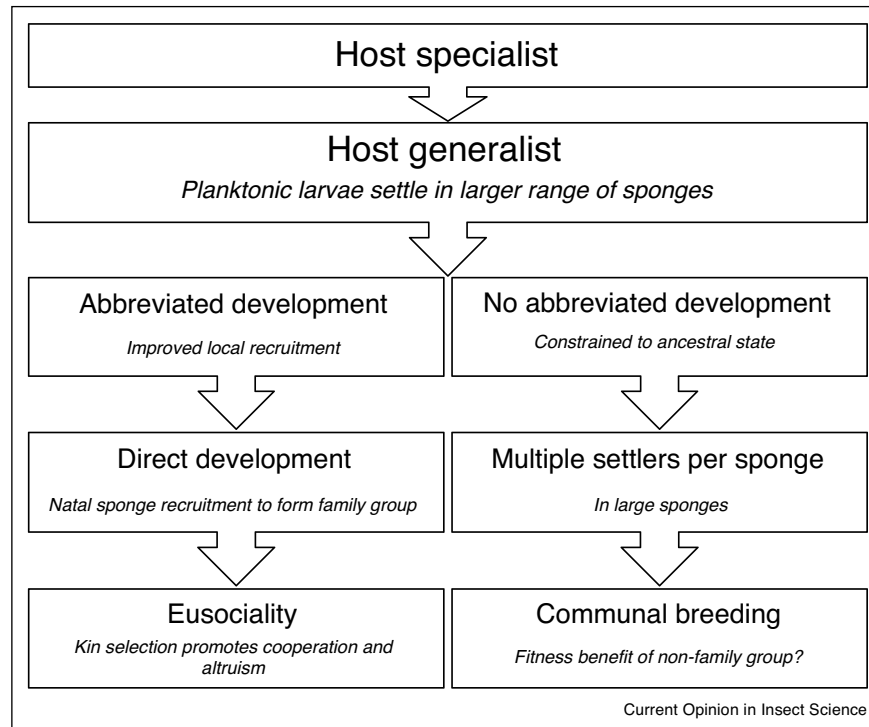
results highlight the importance of exploring both the ecological causes and consequences of sociality [37].

The role of life history in social transitions

Although all *Synalpheus* shrimp live in sponges, a critical factor distinguishing eusocial and non-eusocial species is their mode of larval development. There is an almost complete association between developmental mode and eusociality [9]. That is, eggs from non-eusocial *Synalpheus* species (both pair-forming and communal species) hatch into planktonic larvae that molt and undergo a series of larval stages before settling as juveniles [38]. In contrast, all eusocial species exhibit ‘direct development’, which is an extreme form of abbreviated development where the larval stage is highly reduced to a point that eggs hatch into crawling, benthic juveniles [9,39,40]. These non-dispersing juveniles may delay their dispersal if habitat saturation limits the possibility of independent breeding [41], a phenomenon that will favor the formation of extended family groups and allow kin selection to operate. In species where larvae disperse away from the natal sponge, communal groups could form when multiple juveniles settle in large sponges to form multiple mating pairs, but these groups would have low genetic relatedness, as we have found (Rubenstein and Duffy, unpublished data). In essence, the difference in developmental mode between communal and eusocial species may explain why communal *Synalpheus* species never evolved into eusocial species via the ‘parasocial model’, despite the fact that ancestors of communal and eusocial species likely experienced similar ecological pressures.

Although generally rare in decapod crustaceans, direct development also characterizes species that have invaded freshwater systems from marine ancestors and constitutes a key adaptation to novel environments [39]. Less intense forms of abbreviated development (i.e. various levels of reduction in larval stages that do not result in direct development) are frequently found in marine decapods that live in stressful conditions such as polar waters and the deep sea [39]. Therefore, ecology may be an important evolutionary driver for a reduction in larval stages in decapods. In *Synalpheus*, ecological generalism may have facilitated the change to direct development [28**]. The fact that ecological generalists have a larger local pool of potential sponge hosts than specialists may have initially favored the change toward abbreviated development, where reduced dispersal allowed these species to utilize the higher availability of local hosts. However, after local sponges became completely exploited, competition for available sponges may have become even more intense. In turn, this may have favored the evolution of direct development and the evolution of eusociality, in which cooperation within family groups could have allowed for better defense and acquisition of host sponges in the face of strong interspecific and intraspecific competition for these critical resources.

Figure 3



Hypothesis of the steps toward eusociality and communal breeding in sponge-dwelling snapping shrimp by incorporating knowledge of host ecology and life history.

Communal species, despite having host generalist ancestors, retain the ancestral pelagic mode of larval development (although whether the number of larval stages is reduced remains unknown). This perplexing pattern could be due to physiological constraints that are specific to certain lineages. For example, communal species generally have larger body sizes than eusocial species (Chak and Rubenstein, unpublished data). In crustaceans, larger females tend to have greater fecundity, but abbreviated development typically reduces fecundity because of the high maternal investment in eggs [39,42]. Therefore, abbreviated development may incur a higher cost on fecundity in species with larger body sizes, hence abbreviated development may be more likely to evolve in species with relatively small body sizes. This hypothesis remains to be validated using a complete account of body size, egg size, and fecundity across *Synalpheus* species.

Social synthesis: evolutionary steps toward sociality in snapping shrimp

Ecology and life history are clearly both important to the independent social transitions in *Synalpheus*. Here, we develop a hypothesis that describes the evolutionary steps toward communal breeding and eusociality in *Synalpheus* shrimp (Figure 3). First, sponge host specialist

species evolved to become host generalists, in which their dispersing larvae could settle in a wider range of sponges, a limiting resource for all *Synalpheus* species. Within the route toward eusociality, some generalist species were able to reduce the number of pelagic larval stages to improve local recruitment. Habitat saturation and competition may have further favored a reduction of larval stages and direct development. Finally, recruitment of directly developing offspring into the natal sponge and delayed dispersal allowed for the formation of cooperative family groups and the evolution of eusociality.

Within the route toward communal breeding, some sponge host generalist species retained the ancestral pelagic mode of larval dispersal, perhaps due to phylogenetic or physiological constraints. Large sponge volumes in some host species may have facilitated the settlement and the accumulation of multiple unrelated mating pairs that formed communal groups. Yet, the route toward communal breeding is relatively unclear because we still do not know why these species retain the ancestral development mode and whether there are fitness benefits to group living in these non-kin associations. Ultimately, these questions echo a recent call for further studies of communal species to better understand social evolution more generally [1*].

Conclusions

Most studies of the evolutionary transition toward animal societies characterized by cooperative group living have occurred in central place foragers, not in fortress defenders. Here, we reviewed the evolutionary transitions toward both eusociality and communal breeding in sponge-dwelling snapping shrimp, a group of marine fortress defenders. Because of the social diversity within *Synalpheus* shrimp, social transitions toward communal breeding and eusociality can be examined simultaneously, which is often difficult to do in many insect lineages. Recent studies in snapping shrimp show that the independent evolutions of eusociality and communal breeding [10**] may be driven by different ecological pressures associated with sponge host specialization and volume [28**], as well the evolution of different life history traits related to larval development. These studies show that both ecology and life history can interact to influence the independent evolutionary origins of sociality in snapping shrimp. Thus, considering both ecology and life history [1*], as well as the ecological causes and consequences of sociality [37], will be important for understanding major evolutionary transitions in social behavior.

Conflict of interest statement

Nothing declared.

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