

THE EVOLUTION OF SOCIALITY: PERACARID CRUSTACEANS AS MODEL ORGANISMS

BY

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ABSTRACT

Sociality in peracarids has evolved via two principal pathways, the parasocial road (aggregations of individuals) and the subsocial road (parents caring for offspring), but the factors governing the evolution of group-living are not well understood. Knowing the benefits and costs of group-living is key to understand the evolution of sociality. Herein, I present examples of experimental studies that examined the benefits and costs of group-living in conspecific aggregations (COGs) and parent-offspring groups (POGs). These studies show that peracarids lend themselves to experimental studies. Furthermore, there is a bias towards studies exploring the benefits and few studies have explicitly tested the costs of group-living. Several studies confirmed that individuals in groups are better protected from environmental hazards (stressful conditions and predators) than solitary individuals in both COGs and POGs. However, in very large groups, a tradeoff emerges and individual benefits decrease. Present evidence suggests that increasing resource competition in larger groups may be responsible for this tradeoff. However, other factors (cannibalism and disease/parasite transmission) may also contribute to the increasing costs in larger groups. At present, it is not clear whether and how tradeoffs differ between COGs and POGs, which appears essential to better understand the evolution of sociality in peracarid crustaceans.

INTRODUCTION

The evolution of group living is influenced by the tradeoff between the benefits that individuals gain from cohabiting with conspecifics and the costs they pay when living with others. These benefits and costs faced by group-living organisms depend both on intrinsic (life history) and extrinsic factors (environmental conditions). There is also increasing evidence that ecological

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factors play a major role in the evolution of group-living (Korb, 2008). For example, in many species individuals gathered in groups are better able than single individuals to cope with high abiotic stress or strong predation pressure. High abundance and quality of food resources might also favor group-living, because the capability of individuals to exploit and monopolize food might increase in large groups (e.g., Whitehouse & Lubin, 2005). However, group-living also generates costs. For example, competition for resources may be higher in groups, and if resources become limited, this can result in increased aggression and/or reduced reproductive potential among group members. Also, parasites and diseases may rapidly spread within large groups (Schmid-Hempel, 1998). The tradeoff between benefits and costs determines the potential for social evolution, which is then mediated by the genetic relatedness among group members (Hamilton, 1964).

Many recent studies have focused on the conditions that led to the evolution of eusocial behavior (e.g., Foster et al., 2006; Boomsma & Franks, 2006). However, important insights on social evolution can also be gained from studying more primitive social organisms (e.g., Costa, 2006). Here it will be instructive to study species that inhabit a wide variety of environments with differing selective pressures (for importance of environmental conditions see, e.g., Schwarz et al., 2007; Korb, 2008). Organisms that occur in groups of different degrees of genetic relatedness will be particularly useful, because this allows incorporating the importance of kinship in the model.

The Peracarida (Crustacea) represent a taxon well suited to examine the conditions that govern the initial stages of social evolution (fig. 1). Members of the peracarids occur in a wide variety of environments from the deep sea to dry deserts, and kinship of peracarid groups varies along two extremes: (i) aggregations of unrelated conspecifics, and (ii) parent–offspring groups of closely related family members. These two types of groups also represent the two divergent pathways (parasocial and subsocial) on the evolutionary road towards higher social behavior. Conspecific aggregations (parasocial) have been observed in a variety of peracarid species from both terrestrial and aquatic environments. Members of these conspecific aggregations (COGs in the following) are not related to each other (non-kin) and there is usually no particular group structure and adhesion. In contrast, in parent–offspring groups (subsocial) closely related individuals (kin) cohabit for extended time periods and membership is exclusive, i.e., unrelated individuals are not admitted to these parent–offspring groups (POGs in the following). Since the species that follow either the subsocial or the parasocial pathways live in the same environments,

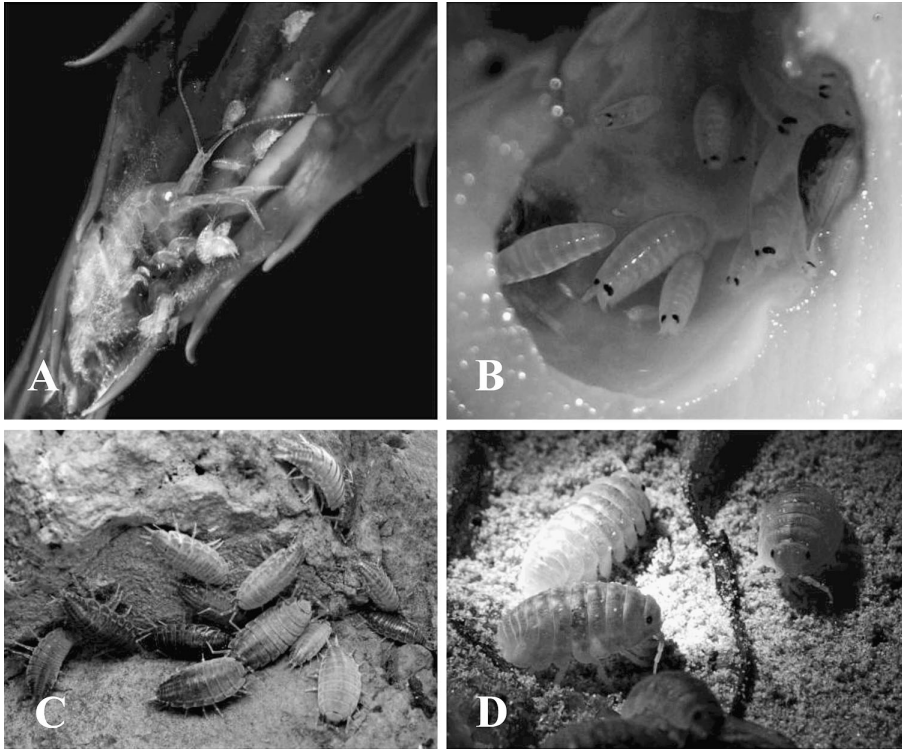


Fig. 1. Amphipods and Isopods in different forms of groups. A, *Peramphithoe femorata* female with offspring in her nest; B, *Parawaldeckia kidderi* in burrow excavated in kelp holdfasts; C, *Porcellio scaber* under rock; D, *Tylos spinulosus* aggregating on food algae in flotsam.

it can be expected that the selective pressures favoring/suppressing cohabitation are similar. However, benefits and costs differ, because group members are either genetically related (subsocial) or not (parasocial). Such differences are expected to have a strong impact on the social evolution of the respective species.

Herein, I will provide examples of peracarid species that live in COGs and POGs where the benefits/costs of group-living have been tested explicitly. Furthermore, I present reports of specific behaviors that might enhance benefits, reduce costs or facilitate group cohesion. For the purpose of this review, the Mysidacea were also included even though their phylogenetic position within the Peracarida is doubtful (Spears et al., 2005). However, mysids share a key life history trait with the true peracarids (direct development) that is known to have a strong influence on social evolution in invertebrates (Costa, 2006). In addition, numerous studies have explicitly tested the benefits and costs of group-living in pelagic mysids (e.g., Ritz, 1994).

TYPES AND SIZES OF PERACARID GROUPS

Conspecific aggregations. — In the aquatic environment, a wide variety of peracarid aggregations is known. In coastal waters, mysid shoals range from tens to millions of individuals (depending on the species). These schools are usually monospecific, but within aggregations age classes often segregate (O'Brien, 1988; but see Modlin, 1990). Dense aggregations of hyperiid amphipods, swirling in tornado-like swarms (Lobel & Randall, 1986) or apparently cleaning sharks (Whitney & Motta, 2008), have also been reported from coastal waters. In freshwater, isopods and amphipods occasionally aggregate in large numbers on the bottom of creeks, rivers or subterranean cave pools (Allee, 1929; van den Brink et al., 1993; Fenolio & Graening, 2009). In marine soft-bottom habitats, some peracarid species reach extraordinary densities, frequently exceeding 10 000 individuals per m² (e.g., Drolet & Barbeau, 2009). Similarly, dense aggregations are also found in wood- or algal-dwelling peracarids, where >10 000 individuals may inhabit a volume of 10³ cm substratum (Thiel, 2003a). On sandy beaches and on land, (semi-)terrestrial isopods and amphipods gather to the hundreds under algal or plant detritus (e.g., Friend & Richardson, 1986; Jaramillo et al., 2006). Occasionally, peracarid aggregations reach extraordinary densities of hundreds of thousands of individuals (Allee, 1929; Paoletti et al., 2008; Fenolio & Graening, 2009).

Parent-offspring groups. — Females are the nucleus of POGs in most peracarid species. Mothers (in rare cases accompanied by the male) typically continue to cohabit with their offspring after these emerge from the maternal brood pouch. POGs are most common in peracarids that inhabit stable dwellings, such as burrows in sediment and wood, self-constructed tubes, algal nests, or biotic microhabitats (sponges, bivalves, ascidians). In these species, juveniles remain with their parents for extended time periods, sometimes several months (Thiel, 2003b). In some free-living species, females also cohabit with their offspring, but usually for shorter periods (days–weeks). Parents caring for subsequent cohorts of juveniles are known from a few peracarid species, but at present no case of overlapping generations (offspring starting to reproduce in the presence of reproductive parents) has been reported (Thiel, 2007). Brood size in peracarids usually varies from 10–100 eggs, and consequently most POGs have similar sizes.

BENEFITS AND COSTS OF GROUP-LIVING

Several experimental studies examined the benefits of group-living in COGs and POGs. Benefits can be enhanced survival of group members due to protection against adverse environmental conditions and predators. Furthermore, individuals in aggregations may have higher growth rates due to more efficient exploitation of food resources.

In swarm-living mysids, Ritz (2000) observed that individual food intake is very low in small groups but then increases in parallel with the number of group members (fig. 2A & B). While food intake remains high in larger groups, there is a tendency that benefits decrease with increasing group sizes, most likely due to increase competition (fig. 2A). Very similar observations were reported for terrestrial isopods: single individuals had substantially lower growth rates than individuals in aggregations (fig. 2B). However, in very large aggregations (> 10 individuals) growth rates significantly decreased, albeit not to levels of single individuals (Brockett & Hassall, 2005). These response curves can be resource-dependent, i.e., the optimal group size is positively related to the abundance or quality of resources (e.g., in mysids, Ritz, 2000). It can be expected that group members are sensitive to changes in resource availability and adjust their gregarious behavior accordingly.

Group-living is also an efficient strategy in alleviating stressful conditions. Under dry conditions terrestrial isopods survived much longer in aggregations than as solitary individuals (fig. 3A; Allee, 1926). These isopods are very sensitive to desiccation, and consequently individuals that suffer from water loss are attracted to conspecifics via smell (fig. 3B; Kuenen & Nootboom,

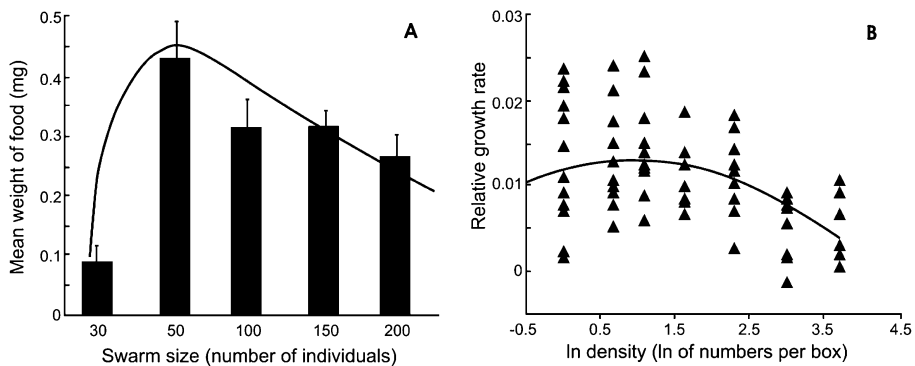


Fig. 2. A, mean dry weight of 10 stomachs of the mysid *Paramesopodopsis rufa* in swarms of different size (after Ritz, 2000); B, growth rates of isopods *Porcellio scaber* maintained at different densities (after Brockett & Hassell, 2005).

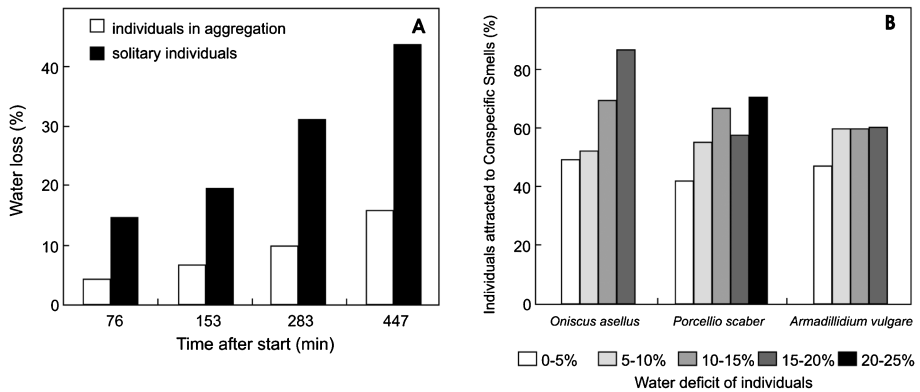


Fig. 3. A, water loss of terrestrial isopods (species not mentioned) that occur in aggregations (10 individuals) or as solitary individuals (data from Allee, 1926). B, proportion of individuals selecting the branch with conspecific odor in a Y-maze (after Kuenen & Nootboom, 1963).

1963). Many COGs are assumed to form as a strategy to overcome stressful conditions.

In POGs, cohabitation of offspring with mothers was shown to result in enhanced growth and higher survival of the juveniles. Aoki (1997) examined juvenile growth rates in several species of caprellid amphipods. Juveniles were raised as orphans (mothers absent) and with maternal care (mothers present). In species that do not usually exhibit maternal care (*Caprella danilevskii* and *C. subinermis*), growth rates did not differ between the two treatments. However, in two of the three species with maternal care (*C. decipiens*, *C. scaura* and *C. monoceros*), offspring growth rates increased significantly when the mothers were present (fig. 4). The author suggested that in *C. scaura* and *C. monoceros* the females are important as attachment substratum for small offspring, which can not yet efficiently grasp to the substrata (hydroids, algae) on which these species are found in nature (Aoki, 1999). Interestingly, in the intertidal amphipod *Parallorchestes ochotensis*, where juveniles remain for long time periods in the female's brood pouch, juveniles under maternal care grew less than control juveniles without their mother (Kobayashi et al., 2002).

Two experimental studies confirmed that maternal care offers effective protection against predators for small juveniles. In *P. ochotensis*, juvenile survival was high in treatments without predators, regardless of maternal care, but in predator presence juveniles with their mothers had significantly higher survival rates than orphan juveniles (fig. 5A; Kobayashi et al., 2002). Very similar results were obtained for juveniles of the burrow-living amphipod *Leptocheirus pinguis*, where the maternal burrow was instrumental in offering protection against predators (fig. 5B; Thiel, 1999).

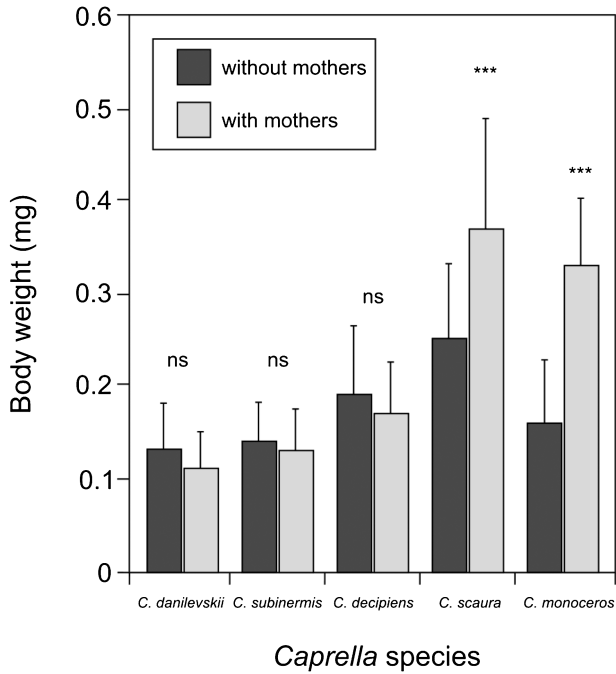


Fig. 4. Growth rates of juvenile caprellids that were reared with and without their mothers (after Aoki, 1997).

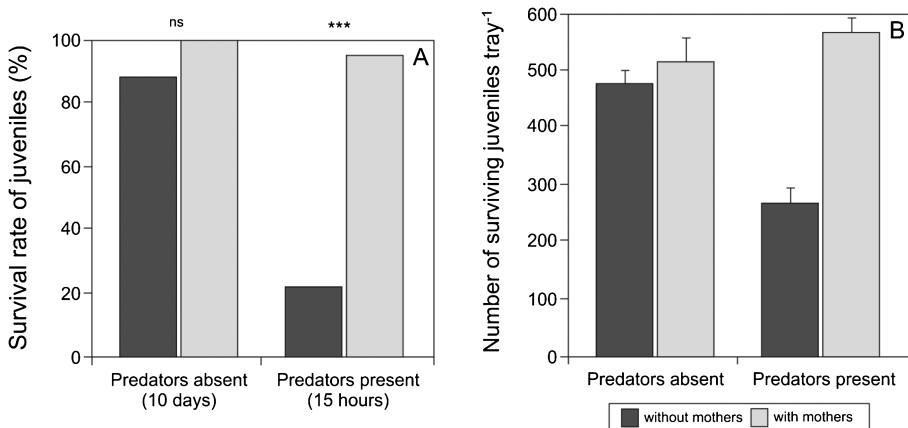


Fig. 5. Survival of juvenile amphipods maintained with and without their mother in presence and absence of predators. A, *Parallorchestes ochotensis*; B, *Leptocheirus pinguis* (A after Kobayashi et al., 2002, and B after Thiel, 1999).

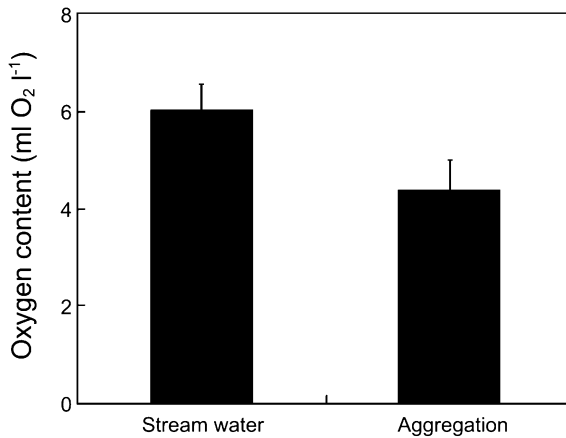


Fig. 6. Oxygen content in stream water above isopod aggregations and of water within dense aggregations of the isopod *Caecidotea communis* (data from Allee, 1929).

Surprisingly, few studies have been conducted to explicitly test the costs of group-living. Costs are generated by resource competition, cannibalism, disease or parasite transmission, contamination, and inbreeding. In very large groups growth or survival may be suppressed, primarily due to competition (see fig. 2A & B). Contamination with excretory products or feces may also cause costs to group members. CO₂-concentrations may increase while O₂-concentrations are expected to decrease in very large and dense groups. Indication for this comes from data by Allee (1929) who showed that oxygen concentrations decreased in dense COGs of the freshwater isopod *Caecidotea communis* (fig. 6), but it is not known whether this led to the disbandment of the aggregations.

BEHAVIORAL INTERACTIONS

Particular behaviors may have evolved to enhance the benefits or to reduce the costs of group-living. These behaviors include strategies to initiate or maintain groups. For example, compact separate schools of mysids mingle quickly (within <2 min) after coming into direct contact (Modlin, 1990). Schools are maintained by inward swimming of individuals from the edge (O'Brien, 1988). Individuals that fell behind were sometimes observed to leap forward and swim towards the center of the school (Clutter, 1969). Several authors emphasized the integrated responses of mysids within large schools (Clutter, 1969; O'Brien, 1988; Buskey, 2000). In several pelagic peracarids authors mentioned whorl-like school formations (e.g., Clutter, 1969) or "tornado-like

swirls” (Lobel & Randall, 1986), in which individual behaviors need to be highly synchronized to ensure coordinated group movements. Vision is important for school maintenance in mysids (Modlin, 1990; Buskey, 2000). Hydrodynamic and chemical cues have often been inferred, but their role in school cohesion is not well known.

Members of POGs react differently to family members than to unrelated individuals, which enhances family cohesion. Female mysids frequently reincorporate lost embryos and larvae into their marsupium (Wittmann, 1978). While females of some mysid species appear capable of recognizing their own offspring, females in most species do not seem to discriminate between own and unrelated offspring, but they show a preference for larval stages that are similar or more advanced than their own brood (Johnston & Ritz, 2005). In some amphipods the females are also able to recognize their own brood in the marsupium (Patterson et al., 2008). Highly specific family cues have evolved in desert isopods, which ensure that only family members are admitted to the parent-offspring burrow (Linsenmair, 2007).

Aggregation behavior can also be context-dependent. For example, terrestrial isopod aggregate quickly under dry conditions but roam solitarily in moist environments (e.g., Allee, 1926). Aggregations form as soon as two individuals come into direct contact and other individuals then join these aggregations. Kuenen & Nootboom (1963) showed that individuals of *Oniscus asellus* that had lost a lot of water have a higher tendency to seek out the smell of conspecifics.

While few studies have explicitly examined the costs of group-living in peracarids there are numerous reports on behaviors supposed to reduce these costs. For example, several behaviors appear to have evolved in response to the high risk of cannibalism in peracarid groups. In some species females synchronize brood release, possibly as a mechanism to avoid that their offspring is cannibalized by conspecifics (Johnston & Ritz, 2001). Synchronization appears to be of higher adaptive value in species occurring in small aggregations (hundreds to a few thousand individuals) than in species with large aggregations; whether synchrony is mediated by extrinsic or intrinsic cues is not known at present (Johnston & Ritz, 2001). Habitat segregation between juveniles and adults is considered another strategy to avoid cannibalism (e.g., Jormalainen & Shuster, 1997; McGrath et al., 2007; Taylor, 2008).

In POGs, active cleaning of the brood and removal of feces and dead individuals from the family burrow (Schneider, 1971) probably has evolved as a strategy to keep parasites and diseases at bay. Females of several species

have been observed to manipulate their small offspring, which was interpreted as maternal grooming (Thiel, 2007). No grooming or cleaning behavior has been reported from COGs; in fact aggregation sites of terrestrial isopods are known for the accumulation of feces.

CONCLUSIONS AND OUTLOOK

This review shows that benefits and costs of group-living may influence the evolution of social behaviors in peracarid crustaceans. The few available studies confirm that group-living can improve survival and growth of group-members, both in COGs and in POGs. Similar as for the benefits the costs of group-living appear to affect both the members of COGs and POGs. Enhanced resource competition could be one of the major costs, but anecdotal observations suggest that parasite/disease transmission and cannibalism can additionally affect health and survival of group members. The fact that benefits started to decrease at large group sizes indicates that there are tradeoffs. These tradeoffs can be species-specific and context-dependent and require investigation. The examples presented herein show that peracarids lend themselves to experimental tests of the benefits and costs of group-living. Most species are relatively small and therefore very suitable for small-scale experiments. Since they have direct development, many species can be easily reared in the laboratory.

Studies on the evolution of social behavior often focus on advanced social behaviors (e.g., Korb & Heinze, 2008). Relatively little is known about the environmental conditions that lead to the initial evolution of group-living (for exceptions see, e.g., Tallamy & Wood, 1986; Costa, 2006). To overcome this gap, comparative studies of species from different environments will be particularly instructive. Future studies should thus focus on the mechanisms that drive the social behavior in peracarid groups in terrestrial and aquatic environments. It appears especially desirable to compare the benefits and costs in COGs and POGs to better understand how genetic relatedness (in POGs) or the absence thereof (in COGs) affects the evolution of social behavior.

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