

Juvenile *Sphaeroma quadridentatum* invading female-offspring groups of *Sphaeroma terebrans*

MARTIN THIEL¹

Smithsonian Marine Station, 5612 Old Dixie Highway, Fort Pierce, Fla 34946, USA

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Female isopods *Sphaeroma terebrans* Bate 1866 are known to host their offspring in family burrows in aerial roots of the red mangrove *Rhizophora mangle*. During a study on the reproductive biology of *S. terebrans* in the Indian River Lagoon, Florida, USA, juvenile *S. quadridentatum* were found in family burrows of *S. terebrans*. Between September 1997 and August 1998, each month at least one female *S. terebrans* was found with juvenile *S. quadridentatum* in its burrow. The percentage of *S. terebrans* family burrows that contained juvenile *S. quadridentatum* was high during fall 1997, decreased during the winter, and reached high values again in late spring/early summer 1998, corresponding with the percentage of parental female *S. terebrans* (i.e. hosting their own juveniles). Most juvenile *S. quadridentatum* were found with parental female *S. terebrans*, but a few were also found with reproductive females that were not hosting their own offspring. Non-reproductive *S. terebrans* (single males, subadults, non-reproductive females) were never found with *S. quadridentatum* in their burrows. The numbers of *S. quadridentatum* found in burrows of *S. terebrans* ranged between one and eight individuals per burrow. No significant correlation between the number of juvenile *S. quadridentatum* and the numbers of juvenile *S. terebrans* in a family burrow existed. However, burrows with high numbers of juvenile *S. quadridentatum* often contained relatively few juvenile *S. terebrans*. The majority of juvenile *S. quadridentatum* found in family burrows of *S. terebrans* were smaller than the juvenile *S. terebrans* that were cared for by their mothers. The results indicate that the presence of *S. quadridentatum* in *S. terebrans* family burrows may negatively affect the duration of extended parental care in *S. terebrans*. It is not known why parental female *S. terebrans* are not able to discriminate against juvenile *S. quadridentatum*. Possibly, the fact that the two species are closely related facilitates *S. quadridentatum* sneaking into *S. terebrans* family burrows.

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Introduction

Animals that live in family groups usually distinguish between related and non-related individuals. Depending on the tightness of the family bonds, non-related

¹Present address: Facultad Ciencias del Mar, Universidad Catolica del Norte, Larrondo 1281, Campus Guayacan, Coquimbo, Chile; e-mail: thiel@nevados.cecun.ucn.cl

individuals are aggressively rejected and excluded from family dwellings. Yet, many organisms have managed to avoid discrimination and are able to gain access to family groups. Among the best-studied associates are those that live in the dwellings of social insects (Wilson, 1971; Hölldobler and Wilson, 1990; Schmid-Hempel, 1998). Associates deceive their hosts by various tactics and subsequently are admitted, overlooked or tolerated in their dwellings. Once in the host dwelling, many associate species may be harmless commensals while others slowly eliminate their hosts and assume ownership of their dwellings (Wilson, 1971).

A variety of marine invertebrates also show subsocial or eusocial behaviour and at least temporarily share dwellings with family members (Duffy, 1996; Thiel, 1999). It could be expected that other organisms attempt to gain access to these communally shared dwellings because these represent protective shelters or food resources. In a eusocial snapping shrimp species, groups of closely related individuals aggressively fend off other snapping shrimp species trying to get access to their dwellings (Duffy, 1996). Family groups consisting of parents and their offspring are also reported from terrestrial and marine isopod species (e.g. Linsenmair, 1984; Svavarsson and Davidsdottir, 1995). In the desert isopod *Hemilepistus reaumuri* Audouin and Savigny, 1826, family members recognise each other by chemical signals and vigorously defend their burrows against non-related individuals (Linsenmair, 1972, 1979, 1984). The occurrence of parent-offspring groups is particularly common among boring isopods (Henderson, 1924; Menzies, 1954, 1957; Messana *et al.*, 1994; Brearley and Walker, 1995, 1996). Here, parents host their offspring in their burrows for extended time periods. Juveniles may even start their own burrows from within the parental burrow (Henderson, 1924; Brearley and Walker, 1995, 1996). Whether parents of these boring isopods are able to recognise their offspring individually is not known but observations by Messana *et al.* (1994) suggest this possibility. In the wood-boring isopod *Sphaeroma terebrans* Bate, 1866, females host their offspring in the terminal end of their burrows (Messana *et al.*, 1994; Thiel, in press (a)). Occasionally, females were observed to 'look towards the outside of their burrows' touching offspring that sought entrance with their antennae and subsequently allowing these juveniles to enter their burrows (Messana *et al.*, 1994). However, females usually sit in their burrows orientated towards the inside and obstructing the burrow with their pleotelson (Messana *et al.*, 1994; Thiel, in press (a)), and are then possibly unable to inspect entrance-seeking juveniles with their antennae.

In many mangrove forests along the Florida coasts, *Sphaeroma terebrans* and *Sphaeroma quadridentatum* Say, 1818 occur together (Estevez and Simon, 1975; Estevez, 1978; Rice *et al.*, 1990). While *S. terebrans* is an active burrower, *S. quadridentatum* is not able to burrow but seeks shelter in crevices, barnacle casings or empty *S. terebrans* burrows (Estevez and Simon, 1975). Roots with many burrows of *S. terebrans* frequently also house large numbers of *S. quadridentatum* that seek shelter in abandoned burrows or root cracks (own observation). During a study on the reproductive biology of *S. terebrans*, on many occasions small juvenile *S. quadridentatum* were found to join female-offspring associations of *S. terebrans*. Herein, I report on these observations in detail.

Material and methods

Burrows containing *Sphaeroma terebrans* were collected each month from a mangrove forest in the Indian River Lagoon, USA (27°32'N, 80°20'W) between September 1997 and August 1998. At the study site, red mangroves *Rhizophora*

mangle L. growing along the shoreline contained large numbers of isopod burrows in their aerial roots (for details see Thiel, in press (a)). Each month, a sample of 40–60 roots was cut at low tide. The isopods were very faithful to their burrows and remained in them until the roots were dissected. Upon return to the laboratory, isopod burrows were carefully opened, and all isopods found within one burrow were preserved in 4% formalin and later transferred to 70% ethanol. Adult isopods were sexed using the presence of penes (males) or the presence of eggs, embryos or oostegites (females). All isopods were measured with the aid of a measurement ocular after stretching them out dorsoventrally with forceps. The two isopod species could be easily distinguished using the shape and surface texture of the pleotelson which in *S. quadridentatum* is rounded at the posterior edge with a smooth surface whereas in *S. terebrans* it is slightly pointed with a rough surface, characters that are already recognisable in early juveniles (see also Estevez and Simon, 1975). The occurrence of *S. quadridentatum* in burrows of *S. terebrans* is analysed in this study. Herein, I term burrows containing at least one adult and several juvenile *S. terebrans* ‘family burrows’ but it should be pointed out that most families only consisted of single mothers and their offspring (Thiel, in press (a)).

Results

Out of a total of 1397 *Sphaeroma terebrans* burrows examined between September 1997 and August 1998, 50 burrows contained juvenile *S. quadridentatum*. At each sampling date at least one female *S. terebrans* was found with *S. quadridentatum* while single male or subadult *S. terebrans* were never found with juvenile *S. quadridentatum* in their burrows. Almost 30% of all parental female *S. terebrans* collected between September 1997 and August 1998 were found with juvenile *S. quadridentatum* in their burrows (table 1). Juvenile *S. quadridentatum* were also found together with female *S. terebrans* that did not host own offspring in their burrows, but the percentage of these cases was very low (table 1). Non-reproductive female *S. terebrans*, i.e. with neither eggs/embryos in their body nor juveniles in their burrows, were never found with juvenile *S. quadridentatum* (table 1). Juvenile *S. quadridentatum* were found in *S. terebrans* family burrows regardless of the presence or absence of male *S. terebrans* in these burrows (Contingency test with Yates’ correction; $p > 0.05$).

The percentage of females that were found with *S. quadridentatum* was high in the fall 1997, decreased during the winter/early spring 1998 and increased again in late spring/early summer (figure 1). The seasonal fluctuation of burrows harbouring *S. quadridentatum* corresponded to that of parental female *S. terebrans* (i.e. hosting their own offspring in their burrows) (figure 1). The numbers of juvenile *S. quadridentatum* in the burrows of female *S. terebrans* ranged from one to eight

Table 1. Number of females *Sphaeroma terebrans* collected between September 1997 and August 1998; females from all months were pooled.

<i>Sphaeroma terebrans</i> females	Total number	Number with <i>S. quadridentatum</i>	Per cent
With juveniles	126	37	29.4%
With embryos	184	8	4.3%
With eggs	234	5	2.1%
With nothing	39	0	0.0%

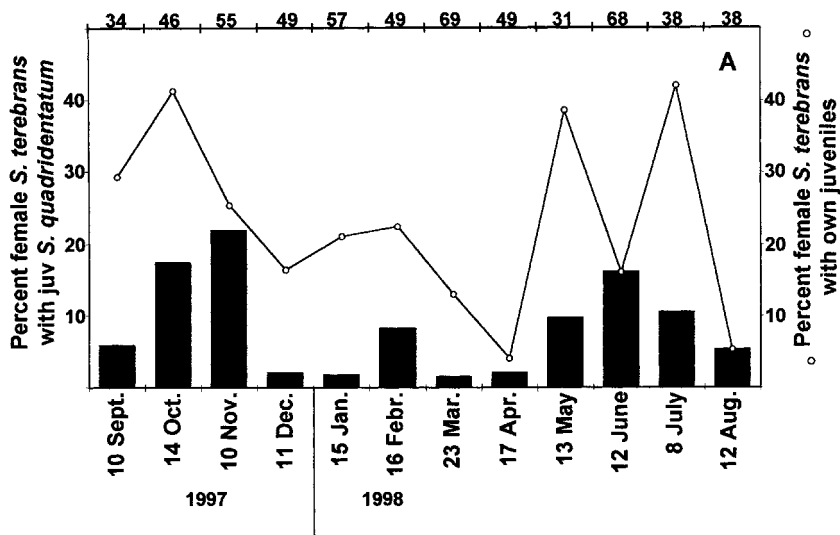


FIG. 1. Percentage of female *Sphaeroma terebrans* that were found with at least one juvenile *S. quadridentatum* in their burrows (histograms), and percentage of parental female *S. terebrans* (i.e. hosting their own offspring in their burrows); numbers on top abscissa—all female *S. terebrans* collected at each sampling date.

individuals per burrow, with an average of about two individuals per burrow (figure 2). For burrows that contained juvenile *S. quadridentatum*, no significant negative correlation between the number of juvenile *S. quadridentatum* and the numbers of juvenile *S. terebrans* in a family burrow existed (Spearman rank correlation; $p > 0.05$). However, low numbers of juvenile *S. terebrans* were often found in

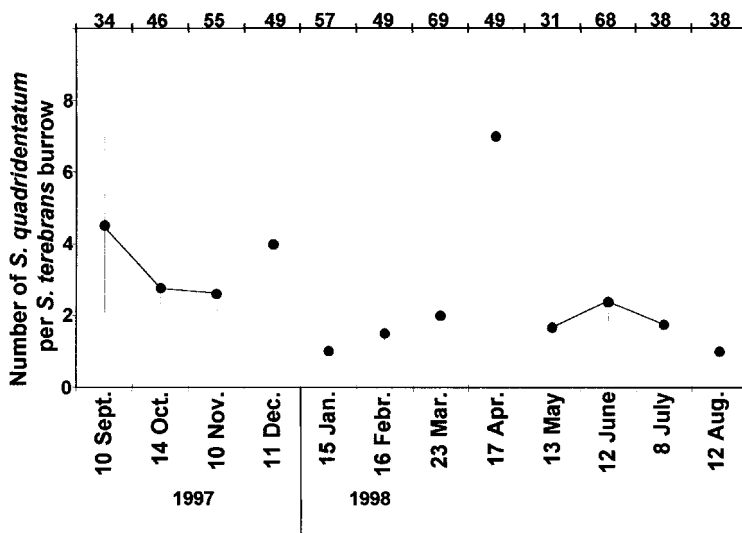


FIG. 2. Average number (± 1 SE) of juvenile *S. quadridentatum* found in those *S. terebrans* burrows that contained *S. quadridentatum*, dots without SE represent sampling dates when only one burrow with juvenile *S. quadridentatum* was found; numbers on top abscissa—all female *S. terebrans* collected at each sampling date.

burrows with high numbers of juvenile *S. quadridentatum* (figure 3). The majority of juvenile *S. quadridentatum* found in *S. terebrans* family burrows was smaller than the juvenile *S. terebrans* that enjoyed maternal care (figure 4).

Large numbers of juvenile *S. quadridentatum* were also seen outside of *S. terebrans* burrows on the mangrove roots. The abundance of *S. quadridentatum* assemblages in root cracks and empty barnacle shells suggests that only a small proportion of the juvenile *S. quadridentatum* find shelter in *S. terebrans* burrows during a given low tide.

Discussion

The fact that juvenile *Sphaeroma quadridentatum* were found in burrows of reproductive female *Sphaeroma terebrans* but never with non-reproductive individuals (single males, non-reproductive females, subadults) indicates that the latter are able to physically exclude juvenile *S. quadridentatum* from their burrows. Juvenile *S. quadridentatum* were able to sneak into family burrows of *S. terebrans* suggesting that parental *S. terebrans* did not exclude these foreign juveniles effectively. The implications of this apparent inability of parental female *S. terebrans* to discriminate against congener offspring are discussed below.

While *Sphaeroma terebrans* is relatively faithful to its burrows once it has established these in the mangrove roots, *S. quadridentatum* is probably much less selective and seeks shelter in cracks, crevices, barnacle shells, and empty *S. terebrans* burrows. *Sphaeroma quadridentatum* often occur in large associations in suitable shelters where they apparently associate during low tides. I consider it likely that *S. quadridentatum* will often seek entrance to occupied *S. terebrans* burrows from which they usually

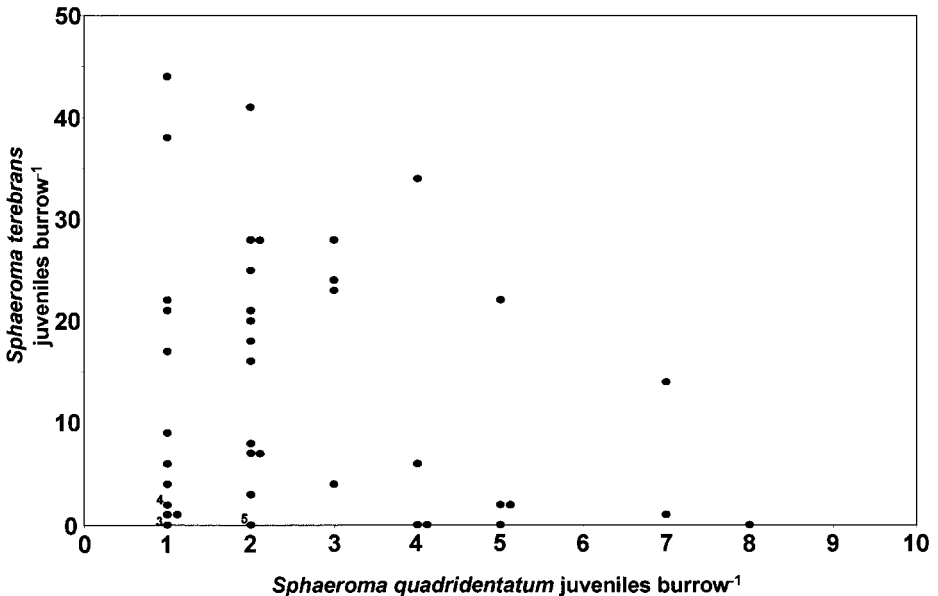


FIG. 3. Relationship between the number of juvenile *Sphaeroma terebrans* and juvenile *S. quadridentatum* in *S. terebrans* burrows containing juvenile invaders of *S. quadridentatum*; numbers besides some dots indicate multiple occurrence of those cases, e.g. five burrows were found with no juvenile *S. terebrans* and two juvenile *S. quadridentatum*; all female burrows containing juveniles between September 1997 and August 1998 were pooled.

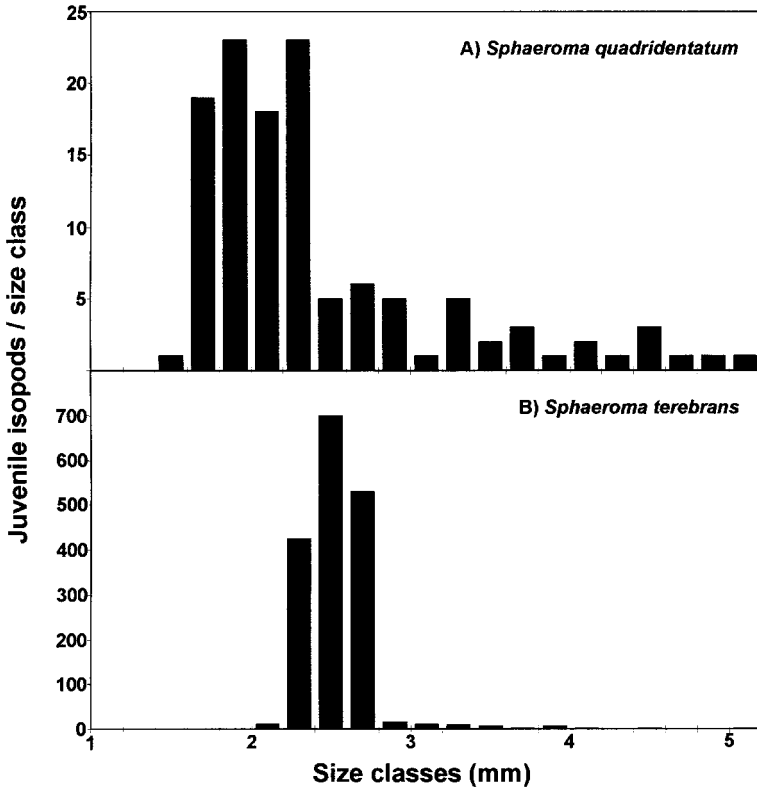


FIG. 4. (A) Number of juvenile *Sphaeroma quadridentatum* in respective size classes found in *S. terebrans* burrows. (B) Number of juvenile *S. terebrans* juveniles in respective size classes found in their mothers' burrows, all juveniles collected between September 1997 and August 1998 were pooled. Note different scales for numbers of *S. quadridentatum* and *S. terebrans*.

are expelled. Occasionally *S. quadridentatum* may remain unnoticed in the outer parts of an active *S. terebrans* burrow, but they are probably unable to enter the parts of burrows occupied by non-reproductive *S. terebrans*. Reproductive female *S. terebrans* apparently tolerate or are unable to exclude juvenile *S. quadridentatum* at the time when they host their own offspring in their burrows. Since most juvenile *S. quadridentatum* found in family burrows were smaller than juvenile *S. terebrans*, it could be that female *S. terebrans* are deceived by the small sizes of juvenile *S. quadridentatum*. While susceptible to burrow invasion by small juvenile *S. quadridentatum*, female *S. terebrans* are increasingly able to exclude potential invaders of larger sizes (figure 3). Figler *et al.* (1997) noted that parental female crayfish *Procambarus clarkii* (Girard) would easily accept foreign offspring when these were at the same developmental stage as their own offspring. They suspected that females do not distinguish between their own and foreign offspring (of similar size) since in nature the possibility of foreign juveniles coming into their burrows may be extremely low (Figler *et al.* 1997). In contrast, individuals from family groups of desert isopods *Hemilepistus reaumuri* and *H. rhinozeros* Borutzkii, 1958 frequently leave and return to their family burrows, thus requiring an efficient system of individual recognition (Marikovskiy, 1969; Linsenmair, 1972, 1979, 1984). Indeed, family members of these

species are well able to recognise each other, and aggressively keep foreign individuals out of their burrows regardless of their size (Marikovsky, 1969; Linsenmair, 1984). Amphipods *Dyopodos monacanthus* Metzger, 1875, *Dyopodos porrectus* (Bate, 1857) and *Dulichia falcata* (Bate, 1857) that usually do not leave their dwellings during extended parental care are able to recognise and expel foreign offspring (Stephan, 1980). In these species, small individuals are frequently found in the water column (Thiel, 1997), and may upon return to the bottom attempt to seek shelter in large family dwellings instead of building their own dwellings. Thus, in these podoceric amphipods, the possibility of foreign juveniles invading families may be high, resulting in the evolution of efficient discrimination against invaders. However, the fact that a caprellid amphipod has been found on a podoceric mud whip (Moore and Earll, 1985) demonstrates that even in these species either discrimination or exclusion may not always be successful.

While animals that live in close social groups have developed mechanisms to recognise group members and discriminate against foreign individuals, many other organisms nevertheless have managed to sneak into these groups. In many cases, sneakers enjoy the advantages of group life but rarely contribute to the well-being of the group. In other cases, group-founders may benefit from the activity of their associates when these, for example, clean or defend the communally shared dwelling or contribute nutrition to their hosts. In the association between the wood-boring isopod *Limmoria lignorum* (Rathke, 1799) and the amphipod *Chelura terebrans* Philippi, 1839 the latter feeds on the faeces of the isopods thereby helping to keep the burrow system clean (Kühne and Becker, 1964). In contrast to this mutual association, small male *Paracerceis sculpta* (Holmes, 1904) sneak into harem colonies defended by alpha males, where the former succeed in producing offspring but do nothing to defend the females (Shuster 1987, 1992). Hence, intraspecific sneakers (small males) invade pre-existing groups to the disadvantage of the group-founders (alpha males). Similarly, parental female *Sphaeroma terebrans* probably do not benefit from the presence of *S. quadridentatum* juveniles in their burrows. The presence and activity of *S. quadridentatum* juveniles in *S. terebrans* family burrows may even be detrimental to the burrow holders. While juvenile *S. terebrans* in undisturbed laboratory experiments remained with their mothers for relatively long time periods and even grew in size during this time (Thiel, in press (b)), in the field many juvenile *S. terebrans* left their mothers at relatively small sizes (Thiel, in press (a)). Juvenile *S. quadridentatum* may occupy space in the family burrow that could otherwise be available for juvenile *S. terebrans*. Additionally, juvenile *S. quadridentatum* are much more mobile and active at a small size than are juvenile *S. terebrans* (own observation). It is possible that the highly mobile juvenile *S. quadridentatum* only stay temporarily in the family burrows of *S. terebrans* (i.e. during low tide) but leave them quickly again to forage outside the burrows. Thus, they may create quite a disturbance in the family burrow where the juvenile *S. terebrans* are relatively sluggish and apathetic during the first time after emerging from their mother's body. Estevez (1978) also commented that 'possibly the young of *S. quadridentatum* may eventually cause burrow evacuation and dispersal' (in *S. terebrans*). Yet, based on the information available at present, it is still too early to judge the effects of juvenile *S. quadridentatum* on the duration of parental care in *S. terebrans*. Experimental studies are required to examine the relationship between these two co-occurring isopod species in detail.

If indeed the presence and activity of juvenile *S. quadridentatum* has negative

effects on the duration of extended parental care in *S. terebrans* as discussed above, the question arises why *S. terebrans* has not evolved efficient behavioural reactions to exclude juvenile *S. quadridentatum* from their family burrows. Both species are closely related to each other, possibly making recognition and exclusion of juvenile *S. quadridentatum* difficult for *S. terebrans*. In this context it is interesting to note that allopatric evolution and subsequent cohabitation has been proposed as the evolutionary pathway leading to social parasitism (Wilson, 1971). Many eusocial insect species are parasitised by closely related, often congeneric, species that cohabit with them in their dwellings (Wilson, 1971). Also, in sphaeromatid isopods, closely related species have been reported to cohabit with boring species (Shiino, 1957; De Loyola e Silva, 1960; Rotramel, 1972), similar to what has been described herein for *S. terebrans* and *S. quadridentatum*. Whether the frequent reports of interbreeding in sphaeromatid isopods (see e.g. Lejuez, 1966; Betz, 1979, 1980) is a consequence of their reduced ability to discriminate against closely related species is presently not known. A close examination of congener associations among subsocial sphaeromatid isopods could not only help to solve this question but also provide further insights in the evolution of congener parasitism in eusocial organisms.

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