Behavioral Ecology of Semiterrestrial Crayfish

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Abstract and Keywords

Like a number of the other crustaceans, burrowing crayfish live in a situation that tends to lead to prolonged associations between mother and offspring, and even overlapping generations in some species. Under these situations, social behaviors are likely to evolve, but at this stage the only ones that have been identified among burrowing crayfish are between mother and offspring, in terms of defense and grooming. Burrowing was a pre-adaptation that has allowed crayfish to move out of open waters onto land, but it has also imposed severe restrictions on their movements and dispersal. The development of social behaviors may compensate for these restrictions to some extent. Present knowledge on the behavioral ecology of semi-terrestrial crayfish is scarce, but initial observations suggest that future studies on the reproductive biology of burrowing crayfish may improve our understanding of social evolution in crustaceans.

Keywords: terrestrial burrows, extended parental care, overlapping generations, dispersal, cohabitation
Freshwater crayfish occupy a range of habitats from open water in rivers and lakes, through the margins of open waters and swamps, to situations that may be kilometers from the nearest surface water. Although they remain dependent on free water, crayfish in these latter situations are almost entirely confined to a burrow and can be described as semiterrestrial rather than aquatic. This lifestyle presents a contrast to that of many of the other crustaceans discussed in this volume but provides some of the conditions under which the evolution of social behavior might be expected via the subsocial route (Wilson 1975).

Being confined to a burrow clearly imposes severe restrictions on the reproductive behavior of crayfish. Opportunities to leave the burrow are often limited by climatic conditions and the risk of predation, and this constrains foraging, mating, and dispersal. On the other hand, the burrow may be seen as a self-contained system that supplies all the animal’s needs. Under these circumstances, there will be selective pressure for the inhabitants to coexist and for the generations to overlap, especially where opportunities for dispersal are infrequent, creating two of the three conditions that have been suggested to be necessary for the evolution of parental care (Wilson 1975, Clutton-Brock 1991; see also chapter 16): the juveniles face harsh physical conditions, are exposed to severe competition or predation, or rely on resources that they are unable to obtain by themselves.

This brief review summarizes the reproductive behavior and ecology of burrowing crayfish and discusses what little is known about the development of social behavior in the group, rather than providing a model for the evolution of social behavior. Because of their burrowing habit, limited information is available about the behavior of semiterrestrial
crayfish; some of what follows has been extrapolated from observations of open-water species.

**Taxonomy and Ecology**

**Systematics**

Freshwater crayfish are found on all the continents except Africa and Antarctica and on a number of oceanic islands (Madagascar, New Zealand, and islands in Melanesia and the Caribbean) (Hobbs 1988). Two phylogenetically well-supported (Scholtz 2002) superfamilies of freshwater crayfish, Astacoidea and Parastacoidea, are found in the northern and southern hemispheres, respectively; Astacoidea currently includes two families, Astacidae and Cambaridae, while Parastacoidea consists of a single family, Parastacidae. The world fauna includes more than 570 species of freshwater crayfish (Fetzner 2003), with local centers of diversity in the southeast of North America and the southeast of Australia, where most of the semiterrestrial species are found. Crayfish are largely absent from the tropics, but some species inhabit New Guinea and the surrounding islands, Madagascar, and Central America.

The world fauna is quite well described at the species level, following recent studies in Australia (Morgan 1986, 1988, 1997, Horwitz 1990, Austin 1996, Austin and Knott 1996, Horwitz and Adams 2000, Hansen and Richardson 2006), but the generic framework of the North American fauna is in need of revision (Fetzner 1996; K.A. Crandall, personal communication). Phylogenetic relationships at the generic and family levels are emerging (Crandall and Fetzner 1995, Crandall et al. 1999, 2000). (p.321) In the Parastacidae, at least, these suggest that high dependence on a burrow has evolved more than once within the family (Crandall et al. 1999).

**Burrowing Habits and Burrow Types**

The colonization of land by the Crustacea has been modest compared with that of other arthropod groups, and among the decapods, the astacidean crayfish have established only a very limited presence on land. Like the other crustacean land colonists (isopods, amphipods, anomuran and brachyuran crabs; Bliss and Mantel 1968), the astacideans have adapted to life on land not only through morphological and physiological changes but also by developments in their behavior. The principal behavioral characteristic that has
enabled crayfish to live independently of surface water has been the further development of their ancestral capacity to construct burrows. While burrowing is also seen in some of the other terrestrial crustaceans, such as the desert crab *Holtthusiana transversa* (Greenaway 1984) and desert isopods (chapter 16), all semiterrestrial crayfish construct burrows that are often complex, and the vast majority are confined to their burrows for most of their lives. Perhaps the only exception is the Lamington spiny crayfish, *Euastacus sulcatus*, which lives in subtropical rain forests in Queensland, Australia. Although it constructs only simple burrows at the edges of streams, it makes extensive excursions on land through the forest to forage, returning to its home burrow (Furse and Wild 2002).

All crayfish burrow to a greater or lesser extent, whether they live permanently in open waters or on land (Berrill and Chenoweth 1982). The burrows range in structure from very simple shelters under rocks or logs in streams and lakes to extensive and complex systems on land that may ramify horizontally for several meters or descend more than 4 meters into the soil. Burrows primarily provide shelter, initially from predation (especially immediately postmolt and during brooding) in open-water species, and increasingly from harsh physical conditions in the more terrestrial species. For some species, the burrow may also supply much of the inhabitants’ food, in the form of plant and animal material (Growns and Richardson 1988, Gutiérrez-Yurrita et al. 1998).

Crayfish have been classified on the basis of their burrowing capabilities, originally by Hobbs (1942). Primary burrowers are those that are restricted to their burrows for the majority of their lives; secondary burrowers wander into open water during rainy seasons; tertiary burrowers primarily live in open water and only occupy burrows during periods of drought, or sometimes in the mating season. In the North American fauna, primary burrowers are found mostly in the Cambaridae, particularly the genera *Cambarus*, *Procambarus*, *Distocambarus*, and *Fallicambarus*. In the Parastacidae, primary burrowers are found in *Engaeus*, *Engaewa*, *Parastacoides*, *Parastacus*, *Tenuibranchiurus*, and *Virilastacus*. 
It is also possible to classify the types of burrow that crayfish construct on the basis of their habitat, particularly their water supply (Fig. 15.1) (Horwitz and Richardson 1986); this approach recognizes that the same species may construct different burrow types in different locations. Type 1 burrows are those found in or at the edges of open water bodies; they may have all their entrances normally under water (type 1a) or some of them normally above water (type 1b). Type 2 burrows are not associated with surface water but extend downward, sometimes several meters, to meet the water table (e.g., in the “prairie crayfish,” *Procambarus hagenianus* and (p.322) related species; Fitzpatrick 1975). These burrows can be found many kilometers from open water, provided there is an accessible water table. Type 3 burrows are also found away from open water, but in this case the burrow does not extend to the water table. Instead, it contains water that has drained into the burrow from the surface and is stored in chambers; these burrows are necessarily found in impervious clay soils. Type 3 burrows were thought to be confined to southeast Australia, where they are constructed by several species in the genus *Engaeus* (Fig. 15.2), but recent work in southeastern North America (S. Welch and A. Eversole, personal communication) suggests that similar burrows may be found there, constructed by species from the genus *Cambarus*. Type 3 burrows (and type 2 burrows in some situations, e.g., peatlands and heavy clay soils) are likely to be much longer lived than type 1 burrows, outlasting many generations of their inhabitants. The characteristics of these burrow types and some of the ecological correlates discussed below are summarized in Table 15.1.

In some situations, crayfish burrows may represent a valuable resource that must be defended, like the dwellings of snapping shrimps (chapter 18) or desert isopods (chapter 16). This is most likely when the conditions do not allow burrows to be readily excavated, as in type 2 and especially type 3 habitats. However, the extensive nature of most crayfish burrows, with multiple entrances, suggests that they are not designed
(p.323) to be as readily defensible as, for example, the burrows of the desert isopod *Hemilepistus reaumuri*, which have only one single opening (chapter 16).

*Figure 15.1* Burrow types (Horwitz and Richardson 1986) constructed by freshwater crayfish. (a) Type 1a and 1b burrows associated with open water. (b) Type 2 and 3 burrows. Drawings by Premek Hamr.
### Morphological Adaptations

Burrowing crayfish show morphological adaptations to life in burrows, and these tend to be exaggerated in the more terrestrial species. Crayfish living in low oxygen situations, which may include burrows in the beds of streams and lakes, increase their gill area by vaulting of the carapace and increasing the volume of the gill chamber, producing a tall narrow carapace with a highly reduced areola, that is, the dorsal area (p.324)

**Figure 15.2** Openings of freshwater crayfish burrows. (a) *Astacopsis tricornis* at the entrance of a type 1a burrow in Lake St. Clair, Tasmania. Photo by Jon Bryan. (b) Type 2 burrow of *Parastacoides tasmanicus* in sedgeland in western Tasmania. (c) Cryptic entrance of type 2 burrow of *Engaewa reducta* in Western Australia. (d) Type 3 burrow of *Engaeus cisternarius* in temperate rainforest, northwest Tasmania. (e) Large “chimney” at entrance of type 3 burrow of *E. orramakunna* in northeast Tasmanian rainforest. Photo by Niall Doran.
Table 15.1. Burrow classification of Horwitz and Richardson (1986) (see Fig. 15.1), with ecological, morphological, and reproductive correlates.
## Behavioral Ecology of Semiterrestrial Crayfish

<table>
<thead>
<tr>
<th>Burrow Type</th>
<th>Water Source</th>
<th>Burrow Development</th>
<th>Range and Typical Genera</th>
<th>Burrow Function</th>
<th>Typical Crayfish Morphology</th>
<th>Brood Size (Range)</th>
<th>Duration of Mother–Young Association</th>
<th>Dispersal of Young</th>
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<tr>
<td>1a</td>
<td>Open water</td>
<td>Simple, usually short and unbranching, under rock or log; all entrances under water</td>
<td>All continents: $^b$ <em>Orconectes</em>, <em>Austropotamobius</em>, <em>Pacifastacus</em>,</td>
<td>Temporary Breeding, predator refuge</td>
<td>Body and claws spiny; claws held horizontally, usually isomorphic</td>
<td>90–1,000</td>
<td>Weeks</td>
<td>Open water</td>
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<tr>
<td>1b</td>
<td>Open water</td>
<td>Simple, openings under water and on land</td>
<td>All continents: <em>Euastacus</em>, <em>Cherax</em>,</td>
<td>Temporary Breeding, predator refuge</td>
<td>Body and claws spiny; claws held horizontally, usually isomorphic</td>
<td>36–126</td>
<td>Weeks</td>
<td>Open water</td>
</tr>
<tr>
<td>2</td>
<td>Water table</td>
<td>Simple to complex; several openings; sometimes with ramifying</td>
<td>N. and S. America: <em>Cambarus</em>, <em>Procambarus</em>, <em>Fallicambar</em></td>
<td>Permanent; sometimes surface excursions to forage</td>
<td>Desiccation, predator refuge; food source</td>
<td>22–108</td>
<td>&lt; 1 year</td>
<td>Overland in wet season (annual)?</td>
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<td>Burrow Type</td>
<td>Water Source</td>
<td>Burrow Development</td>
<td>Range and Typical Genera</td>
<td>Burrow Occupation</td>
<td>Burrow Function</td>
<td>Typical Crayfish Morphology</td>
<td>Brood Size (Range)</td>
<td>Duration of Mother–Young Association</td>
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<td>subsurface tunnels; depth may be &gt; 4 m</td>
<td>Surface runoff</td>
<td>Complex; sometimes with ramifying subsurface tunnels; one to several water storage chambers</td>
<td>3, Engaeus, Cherax, Parastacoides</td>
<td>us, Engaeus, Cherax, Parastacoides</td>
<td>and find mates</td>
<td>isomorphic; tail fan sometimes terminally spiny</td>
<td>13–61</td>
<td>&lt; 3 years</td>
</tr>
</tbody>
</table>

*a* Australian species only.

*b* Freshwater crayfish do not occur naturally in Africa or Antarctica.
between the cervical grooves that define the upper limit of the gill chamber (Holdich and Lowery 1988). The orientation of the chelae is correlated with burrowing habit, at least within the Australian fauna (Riek 1969); open-water species hold the chelae in the horizontal plane, whereas with increasing dependence on a burrow, the chelae adopt an increasingly vertical position, which allows them to be held closely against the carapace, perhaps so that the animal can fit tightly into its tunnels. The chelae of primary burrowers are often dimorphic and bear tufts of long sensory setae; pronounced claw dimorphism implies functional differences between the claws, and while little is known about their function (Horwitz 1990), burrow defense is one possibility. Burrowing crayfish are generally less spiny and tuberculate than open-water species, though terminal spination of the tail fan may be associated with burrowing (Richardson and Swain 2002). Particularly in the strongly terrestrial *Engaeus* species from Australia (Hobbs 1988), but also in some of the North American primary burrowers (e.g., *Fallicambarus devastator*: Hobbs and Whiteman 1991), there is a marked reduction in the development of the abdomen (Fig. 15.3). Among the 34 species of *Engaeus* treated by Horwitz (1990), there is a clear relationship between carapace/abdomen ratio and burrow type (Fig. 15.4). These short-abdomen species do not employ the typical astacuran tailflip, and carrying eggs appears to be the main function of the abdomen. The reduction in abdomen size is weakly associated with a reduction in brood size (Fig. 15.5), but there is no apparent compensation in egg size (Fig. 15.6) in *Engaeus*.

![Figure 15.3 Engaeus orramakunna Horwitz, the Mt. Arthur burrowing crayfish from northeast Tasmania, showing the setose chelae and short](image)

*Figure 15.3 Engaeus orramakunna Horwitz, the Mt. Arthur burrowing crayfish from northeast Tasmania, showing the setose chelae and short...*
Figure 15.4 Relationship between abdomen:carapace ratio and burrow type in *Engaeus* species (data from Horwitz 1990). Many species can be found in more than one burrow type, but they have been allocated to a single type on the balance of the ecological observations recorded by Horwitz (1990).

Figure 15.5 Relationship between abdomen:carapace ratio and egg number (brood size) for 15 *Engaeus* species (data from Horwitz et al. 1984, Horwitz 1990).
species for which data are available (Horwitz 1990). In general, the fecundity of burrowing crayfish seems to be lower than that of open-water species (Lowery 1988). Reproductive Biology

**Figure 15.6** Relationship between brood size and egg volume (scaled by orbit carapace length [OCL]) in nine *Engaeus* species (data from Horwitz 1990).

abdomen typical of *Engaeus* species that construct type 3 burrows. Photo by Niall Doran.
Mating

The life history of freshwater crayfish follows that of many decapods, except that there is no free-living larval stage. After hatching, juveniles remain attached to their mother's pleopods for two or three molts before becoming independent as miniature adults.

Few data are available on the life history and breeding biology of semiterrestrial crayfish compared to the wealth of information available for open-water species, especially those exploited commercially, such as *Procambarus clarkii* (Huner and Barr 1991). On reaching sexual maturity, most semiterrestrial species breed annually, but it is likely that warm climate species produce more than one brood in a year, as open-water tropical species do, while in colder climates breeding may only be biennial. Hamr and Richardson (1994) found that *Parastacoides tasmanicus*, a primary burrower, which lives in type 2 burrows in Tasmanian peatlands, mates in March (austral autumn) and carries eggs during the austral winter. The eggs hatch in late spring (November), and the young stay attached to the female's pleopods until mid-summer. They then remain in the maternal burrow for a further 12 months until the following summer (January), over which time the mother's ovaries mature. The female then (p. 328) mates again in the following autumn, two years after the previous mating. Population surveys showed that approximately half of the females are carrying eggs at any time in winter. Circumstantial evidence suggests a similar pattern in other Tasmanian *Parastacoides* species, though at least one species mates in spring rather than autumn. *Engaeus* species for which evidence is available (Horwitz 1990) mostly appear to mate in spring, though some species from the mainland of Australia (e.g., *E. tuberculatus*, *E. fultoni*) may mate in winter. There is insufficient evidence to assess whether any *Engaeus* species show biennial breeding.

Most North American primary burrowers appear to mate in spring, or in spring and autumn (Hobbs 1981, Hobbs and Robison 1989). Johnston and Figiel (1997) found that *Fallicambarus gordoni*, in Mississippi, mated in late spring and extruded eggs in early autumn or winter, since the bogs in which they live are dry over summer and the animals are inactive during that time. Mating season may depend on
latitude; *F. fodiens* mates in summer–autumn in Ohio (Norrocky 1991) but in May in Canada (Crocker and Barr 1968, Williams et al. 1974).

Hobbs (1981) suggested that semiterrestrial crayfish live solitary lives as adults in isolated burrows, even though these burrows may be in close proximity (Hobbs and Whiteman 1991). However, Norrocky (1991) used burrow-specific traps to sample populations of *Fallicambarus fodiens*, a secondary burrower, and found extensive evidence of burrow sharing and turnover of burrow ownership; every combination of sex and reproductive stage were found together, and *F. fodiens* was also found to cohabit with *Cambarus diogenes*. No equivalent data seem to be available for other semiterrestrial species.

Although females of the open-water species *Cherax quadricarinatus*, when kept in aquaria, apparently visit males for mating when they are sexually receptive (Barki and Karplus 1999), in burrowing crayfish it is generally believed that the males travel to the females' burrows to mate (*Fallicambarus fodiens*, Hobbs and Robison 1989; *F. devastator*, Hobbs and Whiteman 1991; *F. fodiens*, Norrocky 1991). It is likely that males detect female burrows chemically, since sex pheromones have been identified in *Procambarus clarkii* (Ameyaw-Akumfi and Hazlett 1975). In regular surveys of a population of *Parastacoides tasmanicus*, Hamr and Richardson (1994) found that burrow occupancy dropped and males and females were found together in burrows for a two-week period in autumn; females carried spermatophores and eggs by the end of this period, after which males and females were no longer found together.

In *Orconectes virilis*, the male stays with the female in their burrow after mating and over winter (Ameyaw-Akumfi 1976 as cited in Gherardi 2002), while in *Procambarus clarkii* and *P. acutus* male and female may both occupy a burrow during the dry season while the female is carrying eggs, but the male's role is unclear.

Mating behavior in burrowing crayfish has rarely been described (Hamr 1991) but appears similar to that of open-water species (see descriptions in Gherardi 2002, Holdich 2002). Despite the differences in the mechanism of sperm transfer (parastacids lack the modified first pleopod of male Astacoidea), mating in parastacid crayfish is basically the
same as in Astacoidea, but with the deposition of a spermatophore between the bases of the female's fourth walking legs, from which the eggs are fertilized as they are extruded. Thus, there is no apparent mechanism for sperm storage in parastacids, in contrast to the North American Cambaridae, in which the (p.329) spermatophore is deposited into a receptacle, the annulus ventralis, and eggs may be extruded and fertilized weeks or months after mating (Albaugh 1973 as cited in Walker et al. 2002). Walker et al. (2002) present genetic evidence that broods of the stream-dwelling cambarid Orconectes placidus were often sired by two or more males, but no similar data are available for semiterrestrial burrowers.

Once they are cemented to her pleopods, the female grooms the eggs with her thoracic appendages and aerates them by slow movements of the pleopods. The eggs hatch after two to eight months or more depending on species and temperature, and the hatchlings remain attached to their mother's pleopods, using special hooks on the tips of the dactylus of the fourth and fifth pereopods (parastacids) or hooks on the tips of the dactylus and propodus of the first cheliped (Astacoidea). After the second or third intermolt stage, the juveniles start to make excursions from the female's abdomen.
Mother–Brood Interactions

Juveniles of some aggressive open-water species disperse from the mother immediately and show aggression to other juveniles from the start. However, it is likely that all burrowing crayfish spend some time associated with their mother after leaving the pleopods. Juveniles of the secondary burrower *Procambarus alleni* forage in the immediate vicinity of their mother but for a few days return to her pleopods when disturbed (Bovbjerg 1956). To facilitate the return of the juveniles, the female adopts an unusual posture, raising her body with her walking legs and extending her abdomen (Ameyaw-Akumfi 1976 as cited in Gherardi 2002). Juvenile crayfish orient toward other juveniles visually; their return to the female may also be visually controlled since they orientate toward mother-sized objects (Pieplow 1938 as cited in Gherardi 2002).

Brooding cambarid females produce a pheromone that is attractive to the juveniles (Little 1975, 1976). Juveniles will orientate toward water from recently berried females; they cannot distinguish their own mother from other brooding females, but they do distinguish between species (Pieplow 1938 as cited in Gherardi 2002; Little 1975, 1976). Production of this maternal pheromone decreases from the time when the final stage juveniles are on the female, but in *Procambarus clarkii* it can be produced over seven stages of juvenile development, lasting more than three months. Independence from the female develops with size rather than age; among a same-aged brood of *P. clarkii*, the largest animals became independent first, while middle-sized ones occasionally returned to their mother, and the smallest remained on pleopods most of the time (Ameyaw-Akumfi 1976 as cited in Gherardi 2002).

Figler et al. (2001) demonstrated that female *Procambarus clarkii* defended their offspring against invading males in an area around a shelter. This maternal aggression was observed in ovigerous females, those carrying stage 1 offspring and those tending stage 2 offspring, some of which were foraging freely.

Longer term associations between mother and juveniles of burrowing crayfish may be imposed by climatic conditions. *Procambarus clarkii* mothers and juveniles can be confined in the burrow for three months or more by dry conditions (Huner...
and Barr 1991). Juvenile *Fallicambarus fodiens* in Canada are forced to remain with the (p.330) female over winter (Williams et al. 1974). Horwitz and Knott (1983) recorded males of the Western Australian *Cherax plebejus* cohabiting with gravid females and proposed that short-lived family units would be formed before the juveniles disperse during the winter rains.

In primary burrowers, especially those in type 3 burrows, the association between mother and offspring may be much longer. Juveniles of the biennially breeding *Parastacoides tasmanicus* remain in the maternal burrow (type 2) for at least 14 months, living in the terminal chamber (Hamr and Richardson 1994). When the female mates again, the young apparently disperse from the chamber but can still be found, albeit in reduced numbers, in small side burrows and cavities near the top of the burrow. Juveniles of *Fallicambarus gordoni* and *F. fodiens* are found in the maternal burrow (Norrocky 1991, Johnston and Figiel 1997). Horwitz et al. (1984) recorded the presence of four generations (mother plus three year classes, the oldest animals being half to two-thirds the size of the adult) in type 3 burrows of *Engaeus leptorhynchus* in northeast Tasmania, and similarly overlapping generations were found in *E. cisternarius* burrows from northwest Tasmania (Suter and Richardson 1977). This behavior is almost certainly the source of earlier observations of “communally dwelling” *Engaeus* species (Clark 1936a, 1936b, Riek 1969). Hobbs and Whiteman (1991) record the presence together of male, female, and juvenile *Fallicambarus devastator* in burrows in prairie regions of eastern Texas, perhaps as a result of drought, and multiple cohorts have been found in the burrows of *Distocambarus crockeri* in South Carolina (S. Welch, personal communication). Hobbs and Whiteman (1991) did not observe any cannibalism amongst groups of *F. devastator* and noted that a family of another primary burrower, *Procambarus (Hagenides) pygmaeus*, raised in an aquarium showed no maternal–offspring aggression, or offspring–offspring aggression after the juveniles became independent of their mother.

These observations of prolonged mother–brood associations raise the question of how the female’s behavior is modified, since in most open-water species the female will consume her young after the initial few weeks of association if they are confined together. Little (1975, 1976) showed that cannibalism
was inhibited in female crayfish (*Orconectes sanborni, O. virilis, and Procambarus clarkii*) carrying young and suggested that this “maternal” state was maintained by the physical presence of at least some young on the pleopods. Blinded females showed the same response, and increasing the number of young in the female’s water did not maintain the maternal state; further, the maternal state started to decline when the number of young on her pleopods decreased below a certain number, all suggesting that in these species it is the physical presence of the young on the pleopods that induces the maternal state. Females can, however, distinguish dead juveniles at any stage and will eat them (Little 1976).

Since it persists long after the young have left their mother’s pleopods, the prolonged female tolerance in semiterrestrial crayfish must be controlled by some other mechanism than the presence of young on the pleopods. Juvenile open-water crayfish are able to learn that males and nonbreeding females are dangerous, avoiding water conditioned by them after a first encounter (Little 1976). Kinship does not appear to affect the survival of juvenile of the open-water Australian species *Cherax quadricarinatus*, perhaps because the dispersal of the young is normally rapid in the field (Karplus et al. 1995). It remains to be seen whether the lack of aggression between the very closely related animals in type 2 and 3 burrows is chemically (p.331) mediated, or by some other sensory means, or whether, as Hobbs and Whiteman (1991) suggest in *Procambarus (Hagenides) pygmaeus*, it is now genetically controlled.
Dispersal

Direct observations of dispersal by burrowing crayfish are difficult to obtain. When juveniles leave the maternal burrow is unclear, and in some species opportunities for dispersal must be very rare, because of the relatively dry surrounding habitats, reflecting the situation for eusocial mole-rats (Jarvis et al. 1994). A rainy season, when there is surface water, probably provides this opportunity, but even then the chances of establishment in a new burrow are small. In Tasmanian peatlands (an unusual habitat for burrowing crayfish), the construction of new burrows by juveniles seems very rare: over a 10-year period, no new burrow systems (juvenile or adult) of *Parastacoides tasmanicus* were observed in a 432 m$^2$ plot (Richardson and Swain 1991), and it is rare to see the small-diameter burrows of juvenile animals anywhere other than around the entrance of the maternal burrow. However, Growns and Richardson (1988) noted a clear correlation between the volume of the burrow systems of this species and the size of the occupant. Because the creation of new burrows seems to be so rare, and the rate of increase in the volume of adult burrows is very slow (Richardson and Swain 1991), this implies a process of burrow swapping, loosely analogous to shell exchange and eviction by hermit crabs (Hazlett 1981), and this in turn suggests that dispersing juveniles mostly take over the vacated burrows of slightly larger animals. Hobbs and Whiteman (1991) also note a loose correlation between burrow volume and size of occupant in *Fallicambarus devastator* (but in this case, there may be much more rapid burrow turnover).

In wetter habitats in clay or sandy soils, where it is easier for juveniles to establish, new burrows of juvenile animals are often seen (Hobbs 1981), and species in these habitats seem to have innate burrowing behaviors (Grow and Merchant 1980). Hobbs (1981) remarked that he had never seen lateral passages that might have been constructed by dispersing juveniles in the burrows of *Cambarus* (*Hagenides*) species, but Hobbs and Robison (1989) report that *Fallicambarus fodiens* juveniles are often seen dispersing over the surface following rains.

Since the chances of survival of dispersing juveniles are likely to increase with body size, there is probably strong selective pressure on juveniles in the more terrestrial burrowing species in type 2 and 3 burrows to reach as large a body size as possible before attempting to disperse. This will eventually
lead to competition with their mother for food and space within the maternal burrow, which is likely to lead either to the evolution of early dispersal or cooperative foraging with their mother (chapter 14).

Comparison with Other Taxa
If social behavior has evolved in the semiterrestrial crayfish, it has done so in a situation that is more comparable with the eusocial insects (Wilson 1975) and eusocial mammals (Jarvis et al. 1994) than with the aquatic crustaceans, that is, in relatively arid terrestrial environments dominated by vascular plants (chapter 14). Among the crustaceans, the closest parallels are with the desert isopods (chapter 16) and bromeliad crabs (chapter 17). Crayfish that burrow in underwater substrata face quite different conditions than do the semiterrestrial burrowers. Atkinson and Taylor (1988) pointed out that aquatic burrowers gain protection from predators but face problems of hypoxia and hypercapnia, problems that can be relieved by leaving, or ventilating, the burrow. Terrestrial burrowers, on the other hand, while rarely affected by hypoxia, are always challenged by the problems of living in air if they leave their burrow, so their burrows are even more a refuge from desiccation than they are from predation. Consequently, there may be greater selective pressure on semiterrestrial crayfish for coexistence between mother and young, since while the young of open-water species can at least survive the physical conditions outside the burrow, those of semiterrestrial species cannot, except in rare circumstances. Not surprisingly, in most truly aquatic burrowers, mother–offspring associations are of relatively short duration. In the river-dwelling *Pacifastacus trowbridgi*, for example, the female retreats to a shelter or shallow burrow after mating; the young start to make excursions from the female in molt stage 2 and are almost immediately at risk of cannibalism by their mother (Mason 1970). Bechler (1981) observed the brooding behavior of the troglobitic crayfish *Orconectes pellucidus* and found that 17 days after hatching the young began to crawl about their mother's body; 27 days after hatching, they made excursions from the female, and by 40 days they had left completely and the female began to eat them. A remarkable exception is *Paranephrops zealandicus*, a stream-dwelling New Zealand species, in which juveniles apparently remain with their mother for 15 months (Whitmore
and Huryn 1999), an association as prolonged as in many primary burrowing species.

Life in a semiterrestrial burrow entails not only an environment outside the burrow that is more hostile than in the aquatic realm, but also a higher cost of constructing a new burrow. For example, desert isopods can construct burrows only during the rainy period (chapter 16), similar to what has been reported for African mole-rats (Bennett and Faulkes 2000). These time restrictions enhance the value of a burrow, especially during those times when no new burrows can be constructed. Under these circumstances, it may be advantageous for small individuals to remain with their mothers until conditions improve (e.g., with the onset of the rainy season; see chapter 16) or until mothers give up their brooding habitat (e.g., due to death; see chapter 17).

Many aquatic crustaceans of all sizes readily construct burrows in benthic sediments, suggesting that sediment burrows may be less costly to construct than in the terrestrial environment. However, in certain environmental situations, the value of burrows may increase, and not all size classes of a species may be able to construct or maintain these burrows. This occurs where burrows are very deep or excavated in very hard substrata (e.g., wood or rock). Under these conditions, small juveniles may be better off remaining with their parents rather than leaving. When costs of producing a burrow are very high, selection may favor other options for organisms seeking refuge. Many marine crustaceans associate with larger invertebrate hosts (e.g., chapter 12). For example, sponge-dwelling shrimp in the genus *Synalpheus* live in sponges, which represent a highly valuable resource, because they offer both food and protection from predators. These sponges (and other hosts) may be scarce in the environment, however, again favoring long-lasting associations among the inhabitants of a given host (chapter 18).

In summary, the burrow or refuge represents a critical resource for (family-dwelling) semiterrestrial crayfish, as it does for many other crustaceans. Estimating the (p.333) value of this burrow (cost of construction, protection from predators or adverse conditions, access to food resources) would be an important contribution to understanding the evolution of social behavior in semiterrestrial crayfish.
Future Directions
Clearly, there is much to be discovered about the behavioral ecology of semiterrestrial crayfish. For many species, the basic parameters of life history (e.g., life span, reproductive frequency and seasonality, brood sizes and survival) remain unknown, and it is probably unwise to extrapolate from a few species in such a phylogenetically and geographically diverse group.

The degree to which individuals of semiterrestrial species are confined to their burrows, particularly with regard to finding and selecting mates, and the ability of young to disperse from the parental burrow could be investigated indirectly using molecular techniques. However, this will depend on being able to catch animals and relate them to a particular burrow system without destroying the burrow, and to date, burrow-specific trapping has rarely been achieved (e.g., Norrocky 1991, Welch and Eversole 2006).

The importance of the burrow to a crayfish or family group of crayfish needs to be investigated: exactly what resources the burrow provides, whether burrow structure is adaptive, and the degree of competition for burrows in various situations. Some information may be obtained indirectly through correlation of morphological traits, particularly claw dimorphism and morphology, with burrowing habit. Laboratory experiments in artificial burrows may also be useful. It is also important to discover the extent to which the animals depend on the resources within the burrow, how much they forage outside the burrow, and, if so, whether foraging (and burrow defense) is a task performed by particular members of family groups.

Gherardi (2002) noted that *Engaeus* species are likely to be good candidates for studies of parental care. Certainly, the nature of the interactions between mother and offspring and between generations of offspring in type 3 burrows is an intriguing question in the context of social behavior. However, it is particularly difficult to make direct observations of crayfish in their burrows. While the structure of the burrow and to some extent the location of animals within the burrow can be revealed by careful excavation (particularly when the burrow is located on a slope and can be excavated from the side), once it has been excavated it is effectively destroyed. In structurally simple burrows, fiber optic devices may offer
some chance of direct observation, but many type 3 burrows are too large, complex, and ramifying for such devices. Little use seems to have been made of artificial burrows, apart from physiological studies (McMahon and Hankinson 1993, McMahon and Stuart 1995), but they offer some promise if animals can be acclimatized to them.

If it becomes possible to make observations within natural or artificial burrows, the spatial relations between mother and brood can be investigated. When burrows are excavated the female is usually found close to the brood, but it is unclear whether this is the normal relationship or whether the adult animal has merely been driven to the lowest point of the burrow by the disturbance during excavation. It is clearly of interest to know whether crayfish mothers tend their brood in the complex way that bromeliad crabs do (p.334) (e.g., Diesel 1992; see also chapter 17) or whether the overlapping of generations is simply a forced cohabitation as the animals await an opportunity to disperse.

At present there is no direct evidence to suggest that burrowing crayfish provide food for their brood; indeed, dietary information of any sort is scarce. It seems likely that type 3 burrows supply most of the requirements of their occupants (Suter and Richardson 1977), but Growns and Richardson (1988) noted that Parastacoides tasmanicus collects sections of the leaves of sedges from the surface and stores them underground. Juvenile P. tasmanicus have a higher proportion of animal food in their diet, but it is unknown whether this is provided to them by their mother.

Rearing broods of burrowing crayfish can be difficult, perhaps because laboratory conditions do not provide the food resources available in a burrow. But if broods can be reared, simple laboratory experiments will show the relationship between burrowing crayfish females and brood of different ages and the sensory modes that mediate coexistence between them. It would be of interest to compare the duration of recognition of the brood in females from a series of species across the range of burrow types: it should be expected that, in species from habitats where burrows are difficult to construct (e.g., drier habitats, harder substrates), mothers and offspring would remain together for longer time periods.

Summary and Conclusions
Like a number of the other crustaceans discussed in this volume, burrowing crayfish live in a situation that tends to lead to prolonged associations between mother and offspring and, in the case of primary burrowers in type 3 burrows, overlapping generations. Under these situations, social behaviors are likely to evolve, but at this stage the only ones that have been identified among burrowing crayfish are between mother and offspring, in terms of defense and grooming. Burrowing has been a preadaptation that has allowed crayfish to move out of open waters onto land, but it has also imposed severe restrictions on their movements and dispersal. The development of social behaviors may compensate for these restrictions to some extent. Although these are interesting possibilities, studying social behavior in situ in these species is always likely to be difficult because of the depth and complexity of their burrows.

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