The Social Breeding System of the Jamaican Bromeliad Crab
Metopaulias depressus

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Abstract and Keywords

The Jamaican bromeliad crab *Metopaulias depressus* lives exclusively in the water-storing leaf axils of bromeliad plants, which provide a supporting microclimate, safety, food, and are expandable and defendable resources. It is suggested that the species evolved extended parental care to ensure reproduction in this scattered microhabitat. Behavioral traits observed in the bromeliad crab are highly suggestive of eusocial behavior. It lives in large colonies consisting of the colony mother and her offspring. Older offspring participate in colony defense, and young adult females stay in their natal colony as subordinate (non-reproductive) females, with the prospect of inheriting their mother's bromeliad as a breeding habitat. Thus, the bromeliad crab has evolved traits that are characteristic of eusocial and cooperatively breeding species. It displays a high degree of sociality that is unique among
crabs and represents the pinnacle of a remarkable and swift social evolution from a non-social marine ancestor.

*Keywords:* extended parental care, overlapping generations, defense, cooperation, colony inheritance

(p.366) In most brachyuran crabs, brood care appears to be limited to the care for the eggs carried under the female's abdomen. Interactions between the mother and larvae or young are extremely rare. One major impediment for brood care to evolve in crabs is their predominant reproductive mode via planktonic larvae. The larvae of marine crab species—except a very few species with direct development (see Rabalais and Gore 1985)—are swept away from their mothers immediately after hatching. The same applies for land-living crabs that retain a marine planktonic development (e.g., Gecarcinidae).

With the colonization of freshwater and terrestrial habitats, most crab species abandoned planktonic larval development because of the unfavorable conditions in the available freshwater habitats (osmotic pressure, downstream transport, predation). Large vitellogenic eggs and a direct development evolved in various lines of freshwater and terrestrial groups independently (see Diesel et al. 2000). The miniature crabs hatching from the eggs usually remain attached to the mother for several days before they disperse. In these species, there is opportunity for brood care to evolve. However, in only a few of the presently studied species, the young and mothers remain together for a protracted period. A common trait of these insufficiently studied species is their distinct breeding habitat: they live in particular microhabitats, in which the mother and the young are safe from predators or find a supporting microclimate in otherwise adverse surroundings. Examples of crabs that use such microhabitats are *Sesarma jarvisi* breeding in the shells of large land snails (Diesel and Horst 1995), *Potamonautes raybouldi* living in water-filled tree holes.
The Social Breeding System of the Jamaican Bromeliad Crab *Metopaulias depressus*  

(Bayliss 2002), and *Metopaulias depressus*, an obligate inhabitant of water-storing bromeliads (Diesel 1989). In these nestlike breeding habitats, the offspring remain with the mother because conditions in the nest are more favorable than elsewhere.

The bromeliad crab *Metopaulias depressus* Rathbun 1896 is one of 10 described endemic species of nonmarine crabs from the Caribbean island of Jamaica. Mothers and offspring of this species live together in the water-storing leaf axils of large bromeliads (Diesel 1989). Large bromeliads of the species *Aechmea paniculigera*, which qualify as breeding sites, live for several years and represent a stable and reliable water source, even during prolonged droughts. They provide the food resources to support large crab families, water, and shelter from predators and are expandable at the same time. Alexander et al. (1991) proposed that extended parental care and occupation of particular microhabitats or nests, which are safe, provide food, and are expandable, are common preconditions for the evolution of eusociality. Small-colony eusocial insects and cooperative breeding vertebrates share the traits of (1) overlapping adult generations or delayed dispersal from the natal group, (2) reproductive division of labor or reproductive suppression, and (3) cooperative or alloparental care of young (Michener 1969, Wilson 1971, Sherman et al. 1995, Lacey and Sherman 1997, Choe and Crespi 1997). The results of earlier studies show that *Metopaulias depressus* combines the traits of extended parental care and inhabiting and defending a well-maintained nest, which both favor the evolution of advanced social life (Alexander et al. 1991, Crespi 1994). In this contribution, we focus on the question whether the bromeliad crab has followed the evolutionary route that Alexander et al. (1991) predicted for species showing these life history features and evolved traits, characteristic of advanced social species. We specifically study (1) colony composition, dispersal, and the evidence for overlapping generations; (2) the existence and potential (p.367) breeding activity of subordinate adults in a colony; (3) territory/nest defense by adult and juvenile colony members; and (4) alloparental care of broods. In addition to a summary of published information, we present previously unpublished results.

The Model Organism: *Metopaulias depressus*
General Biology

The freshwater and terrestrial crabs endemic to Jamaica (family Sesarmidae) are descendents from a marine ancestor that colonized Jamaica about 4.5 million years ago (Schubart et al. 1998). While their closest relatives are marine species with a larval development in the marine plankton, the Jamaican endemics have an abbreviated larval development in fresh water and thus live in independence from the sea. These Jamaican crabs occupy various ecological niches, such as rivers and streams, mountain rain forests, limestone caves, and bromeliad plants (Diesel et al. 2000).

The bromeliad crab is the most unusual of these endemics in terms of habitat choice. The crab is an obligate inhabitant of bromeliad plants. Its life history, morphology, and physiology are adapted to life on bromeliads. The crabs measure up to about 80 mm in width, including the legs (20 millimeters carapace width [mm CW]) and have a dark brownish red color resembling leaf litter and a depressed flat body adapting them to better fit between the narrow leaf bases of the bromeliad plants. Despite their terrestrial habits, bromeliad crabs require access to fresh water for breathing and breeding, which they encounter in the water retained in the leaf axils of the bromeliad. In general, the bromeliads provide all the essential resources in an otherwise hostile environment: water for gill respiration, molting, and reproduction, but also food and, in the narrowing leaf axils, shelter against various predators such as lizards or birds. The bromeliad crab occurs in the central and western mountainous parts of the island, for example, in Cockpit Country, where locations with patches of relatively high bromeliad densities are common. The selected bromeliads, usually Aechmea paniculigera and Hohenbergia species, grow in locations with high precipitation (Laessle 1961, Diesel 1989).

Despite providing all the crabs’ needs, the quality of bromeliads as habitat for bromeliad crabs varies considerably. Plants can roughly be categorized as follows: (1) small plants with few leaves and a low capacity to store water, mostly of the genus Hohenbergia, which are usually uninhabited; if they harbor a crab, then usually a single, not fully grown individual; (2) medium-sized plants with several leaf axils holding water, which may contain one or a few juveniles or adults, but rarely breeding females—adult males usually live in this plant category (Diesel 1989); (3) high-quality, large, ground-borne
and epiphytic bromeliads, usually the species *Aechmea paniculigera*, which measure on average 1.5 m in diameter between the tips of the leaves, have up to 22 rainwater-filled leaf axils, and can store up to 4 liters of water from rain and dew (Fig. 17.1a). These are usually occupied by breeding females, which prefer the largest bromeliads (Diesel 1989). Most of these large bromeliads grow on the ground and up to about 3 meters on the trunk of a tree. Only occasionally, females breed in the canopy 20 meters above ground. Large *A. paniculigera*, which qualify as breeding sites, live for several years and represent a stable and reliable water resource (p. 368) even during long periods of drought because they collect dew as well as rainwater. Most of these large *A. paniculigera* grow from strong old rhizomes, which rapidly produce a new plant (clone) about every three years.

**Figure 17.1** (a) Large terrestrial bromeliad, *Aechmea paniculigera*. These plants are growing as clones from a rhizome. Rhizomes might be decades old and constantly grow to large plants at the same location. Sprouts grow rapidly to a large plant after the older clone has flowered and died. (b) Nursery axil with bromeliad crab (*Metopaulias depressus*) larvae. This is one of one to two dozen water-holding axils on a plant. The nursery axil has been cleared of leaf litter and debris by the mother crab. (c) Mother crab with last brood. The young crabs stay in the nursery axil for up to three months and are cared for by the mother. Later they disperse to other leaf axils over the plant. (d) The mother has
Bromeliad crabs rely entirely on the food resources on their host plant, because they search for food exclusively on the plant (Diesel 1989). Food consists of (1) plant material and insects that are caught between the long leaves of the bromeliad and funneled into the water-filled axil; (2) the organic matter and associated aquatic fauna in the leaf axil; (3) the leaf-litter—associated fauna, such as millipedes, in the lower leaf axils that have lost their capacity to hold water; and (4) smaller invertebrates that visit the plant, for example, in search for water. There is a strong positive correlation between the size of an *A. paniculigera* and the numbers of leaf axils, the amount of water stored, and the amount of available nutritional resources (Laessle 1961, Diesel 1989). As the bromeliad plant grows, the numbers of leaf axils and the associated resources increase, too. The bromeliad crabs continue to grow throughout their life, and female fecundity increases with body size (Diesel 1989). Hence, nest size and the amount of resources increase with every breeding, since the crabs usually remain on the same plant throughout their reproductive life. Therefore, the size of bromeliads is proportional to their quality and suitability for raising large broods. Since large bromeliads are scarce, there is probably strong competition among crabs for these resources.

| Resource Availability | killed and deposited a beetle in the nursery with the young crabs. |
Breeding Biology

*Metopaulias depressus* breeds annually; in the Cockpit Country, the breeding season starts in December and January, when the males leave their bromeliad to pay visits to the females in their vicinity for mating. Females start to produce eggs in January. The large vitellogenic eggs (20–100 eggs per brood, depending on female size) are carried under the abdomen, where they develop for about 10–12 weeks and then hatch (Diesel 1989). All the larvae are released together into one of the water-filled leaf axils, the so-called nursery axil, holding on average 240 milliliters of water (Fig. 17.1b). Female reproduction is relatively synchronous within one area, and most females release larvae within one to two weeks (Diesel 1989). The larvae develop within 13 days into small juvenile crabs (Fig. 17.1c; Diesel and Schuh 1993). For up to three months, mothers defend their offspring from predatory damselfly larvae and spiders, provide food, and improve the microclimate of the nursery axil by enhancing pH, calcium, and dissolved oxygen levels (Diesel 1989, 1992a, 1992b, 1997, Diesel and Schuh 1993).

After about three months, the young crabs start leaving the nursery axil and disperse over the other axils of their natal bromeliad. After one year, they have reached about 7–10 mm CW and belong to cohort 1 (C-1). Although they hatched on the same day, the body size within the C-1 may now vary considerably.

*Metopaulias depressus* attains sexual maturity at about 12 mm CW in males and 13 mm in females (Hartnoll 1964; R. Diesel, unpublished observations). Sexual maturity in females is marked by a distinct “molt of puberty” in which they develop genital openings, change the shape of the abdomen, and modify their pleopods to facilitate attachment of eggs. Likewise, males develop functional gonopods. To determine sexual maturity in the 11–14 mm CW size group, the individuals have to be removed from the bromeliad, except females that carry eggs, which remain visible under the abdomen for about 2.5 months. After the eggs have hatched, some empty egg cases remain attached to the pleopods underneath the abdomen until the next molt, allowing identification of these females as reproductives.
The maximum reproductive lifespan of a female is about three years. Therefore, she can produce about three broods during her lifetime. This coincides with the life expectancy of single shoots of the preferred bromeliad *A. paniculigera*, which exists as a grown plant for about three years, flowers, and then dies (R. Diesel, unpublished observations). Simultaneously with the inflorescence, a lateral shoot (clone) is produced at the base of the dying plant, which grows rapidly and later offers a good-quality territory at the same location within less than a year, which may then be available to a daughter of the previous breeding female.
(p.370) Objectives
For *M. depressus*, bromeliads comprise a microcosm providing a safe place from predators, a favorable microclimate, and all resources the crabs need for life, but suitable large, unoccupied bromeliads are in short supply. Animals living under similar conditions of habitat limitation frequently refrain from dispersing and have evolved an advanced social organization involving cooperation among groups of relatives, many of which do not breed (Alexander et al. 1991, Queller and Strassmann 1998). Earlier work has shown that the bromeliad crab shows extended parental care and that offspring remain for a protracted period on the natal plant, forming family groups (colonies), consisting of a mother and her young from more than one brood (Diesel 1989). Based on these findings, we here investigate the presence in the bromeliad crab of several conditions and behaviors frequently found in eusocial or cooperative breeding species (see Crespi 1994), namely, overlap of generations, alloparental care, and cooperative colony defense.

Overlapping adult generations and nonbreeding adults are characteristic of many eusocial and cooperatively breeding species. Here, we describe colony composition and the dispersal of young crabs from the natal colony. Do overlapping generations occur in bromeliad crab colonies? When do young females become sexually mature, and how do they breed for the first time?

A second trait common in eusocial species, defense of the nest or colony against unfamiliar conspecific invaders, was studied in a set of experiments. Firstly, we investigated whether bromeliads are defendable resources. To a resident female, the highest risk to lose its territory comes from other females that search for a breeding site. Therefore, we studied whether females can defend their nest against other females. An important predisposition for defending the colony is that invaders were recognized as nonmembers by the colony members. These experiments included also interactions between older (C-1) juvenile crabs from other colonies versus the colony mother and versus the older juveniles of the focal colony. For resident C-1 individuals, the participation in colony defense could be their contribution (payment) for staying in the nest.
Cooperatively breeding or eusocial species frequently show alloprenental care. In this context, we were interested in whether older C-1 young of the bromeliad crab help their mother in caring for the brood or in colony defense. Field experiments to address these questions in detail are difficult to perform. Hence, we concentrated on the more general question, whether the most recent brood may benefit from the presence of older C-1 young in the colony.

At the end of this chapter, we review our findings and discuss the social system of *M. depressus* with respect to our new results. Finally, we briefly review the biology of other crab species that might be possible candidates for an advanced social organization worth studying, and we point out open questions and future studies that should be addressed to better understand the social biology of the bromeliad crab.

**Colony Structure and Social Behavior of *Metopaulias depressus***

**Colony Composition and Size at Dispersal**

Composition of bromeliad crab colonies was studied in the mountains of the Cockpit Country (Trelawny) during several field seasons, usually in spring, from 1986 to 1999. Here, we define a colony as the group of crabs found on a single bromeliad plant. All individual crabs from 181 dissected bromeliads were counted and the carapace width measured with a digital caliper (±0.05 mm). Crabs larger than 6 mm CW were sexed and the reproductive status noted. Age cohorts were distinguished by size, the latest brood being referred to as cohort 0 (C-0) and previous broods referred to as cohort 1 (C-1), which consists of individuals that must be at least one year old.

The results show that at least two successive broods coexist on a single bromeliad and form colonies consisting of presumed family groups (Fig. 17.2). Individuals of different age cohorts were distinct by their size. C-0 juveniles usually attained 2–4 mm CW in May–June, whereas C-1 individuals were larger than 7 mm CW. There exists a pronounced body-size variation within C-1 (17.1−226.3%, n =58 colonies with more than five C-1 members of known size). This variation of up to 226.3% suggests that C-1 consists of crabs one and two years old, but no attempt was made to further subdivide C-1, due to a continuum in body sizes, possibly a consequence of differential growth. The largest of 181 studied colonies consisted of a very...
large reproductive female (20.2 mm CW), 71 C-0 offspring of around 3 mm CW, and 12 C-1 offspring of 6.2–14.6 mm. In 83.4% of the colonies, 1–25 older young (C-1) were present in addition to the most recent brood (C-0).

All colonies invariably held only one single reproductive female, ranging in size from 13.2 to 20.3 mm CW. In addition to the single reproductive colony mother, 21.5% of the colonies held one and in few cases two smaller crabs of 13.2–14.6 mm CW that were large enough to reproduce, as known from solitary females of this size with eggs (see below). Our comparisons within this smaller size class revealed that 53% \( (n = 15) \) of the solitary females were carrying eggs, whereas similar-sized females in a colony never carried eggs or showed signs of reproductive activity \( (n = 10; \chi^2 = 7.8, df = 1; P = 0.008) \). This means that mature females did not reproduce in the presence of the dominant colony mother, thus acting as subordinate females. Females of about 13–15 mm CW that are carrying eggs are breeding for the first time (primiparous) in their lives. An analysis revealed that only 31% \( (n = 35) \) of these egg-carrying young females were residing alone on a bromeliad. Most likely, they had dispersed recently from their natal colony, in an effort to

Figure 17.2 Bromeliad crab (Metopaulias depressus) colony collected in 1998 from a large Aechmea paniculigera. The colony mother (top right) is the only reproductive female, with an adult nonreproductive female, possibly her daughter (top left), the most recent brood (C-0, relatively small because of an overall high brood mortality in 1998), and the offspring of about one year of age (C-1).
start a new colony as foundresses. The other 69% of the small primiparous females were found on a bromeliad together with 1–12 smaller C-1 individuals. In this case, it seems most likely that the larger reproductive colony mother must have died and the primiparous female took over the bromeliad as an heiress. Alternatively, this female could be an invader that dispersed from another colony and now tolerates the unfamiliar juveniles in her new breeding territory. This, however, seems highly unlikely because inhabited bromeliads are widely dispersed and the risk of facing injury or death when invading a colony occupied by another female is very high. Much more probable is that a daughter of the former colony mother takes over the nest location together with her siblings.

Staying Home or Leaving

How long do young crabs stay in their natal plant? Because the exact age of a crab cannot be ascertained, we used body size as an approximation. To determine the sizes at which crabs disperse from maternal colonies, we studied the size distribution of the crabs from 329 bromeliads dissected in the period of March to June over several years. The body sizes of the crabs in colonies were compared with those found solitary on bromeliads, assuming that solitary individuals must have dispersed from their natal colony.

The size distribution of colony members shows a marked decline in the number of individuals larger than 9 mm CW (Fig. 17.3). The smallest solitary individuals (p.373) found were 8 mm CW; the highest abundance of solitary individuals is between 9 and 10 mm CW. There was no marked difference in this pattern between sexes. Hence, the young crabs appear to remain with their mother for at least one year, the time necessary to reach the minimum size observed in solitary juvenile crabs. Then some individuals may disperse, whereas others stay.
Colony Defense
Do resident females defend their bromeliad against colony nonmembers?
Three experiments were performed to study the reaction of the resident female against unfamiliar adult males, females, and juveniles. Most experiments were conducted in the field. Only few colonies were brought for observation into the laboratory over the years, because it is difficult to transport the large plants without damage.

Figure 17.3 Frequency distribution of body sizes (CW) of crabs found in colonies or solitary on bromeliads. The decline in frequency of individuals larger than 9 mm CW in colonies indicates the size at which some individuals disperse. These are found solitary on bromeliads.
Resident Female Versus Unfamiliar Adult Crabs

The behavior of the resident female toward intruding large adult females was investigated in 11 colonies (one resident female was used twice against different invaders) that were transported to the laboratory in the years from 1996 to 1999. Resident females ranged from 15.9 to 19.8 mm CW, and the nonfamiliar females that were released into the colony were 15.4–19.4 mm CW in size. The invaders were released onto the outer tip of the leaf of the axil inhabited by the resident female. For distinction, invaders were marked with a black marker dot on the carapace. Following the release, the crabs were observed until one left the axil. In some cases, the axils were videotaped to document the interactions between the two females in later analyses. To study the reaction of the breeding female toward males, we released a large nonfamiliar male in each of four colonies during the nonbreeding season.

In the staged contests, the colony mothers defended their nest vigorously. Female and male invaders usually moved very slowly downward into the axil with the resident female. Within 30 minutes, all resident females invariably attacked and expelled the intruding females from the axil (sign test, \( p < 0.001, n = 11 \)), even when the invader was larger than the resident \( (n = 8) \). For an invader, there is a high risk of becoming injured during fights. One intruding female lost walking legs, one lost both chelae, and two females fled and leapt from the plant when attacked by the resident female. Similarly, resident females attacked and expelled the intruding males \( (n = 4) \). The killing of invaders was observed by chance in two colonies in the field (R. Diesel, unpublished observations): in each case, an adult individual that had previously not been recorded from the colony was killed and cannibalized by the resident female.

Resident Female Versus Cohort-1 Individuals

The behavior of colony mothers toward unfamiliar and familiar C-1 individuals was studied in June 1999 in the field and in the laboratory. Fourteen individuals ranging from 7.6 to 14.2 mm CW were collected as colony nonmembers from distant bromeliads. One C-1 individual was collected from each of six focal colonies as familiar colony members (ranging from 8.9 to 12.4 mm CW). All C-1 individuals were marked, and each
released into a different nonfamiliar \((n = 14)\) or familiar \((n = 6)\) colony. (p.374) The individuals were observed continuously for the first 30 minutes and afterward by frequent controls for up to several days.

The result of this experiment suggests that the colony mother is capable of distinguishing between colony members and unfamiliar young crabs. In the experiment in which familiar C-1 individuals were released into their natal bromeliad, they were not attacked, remained in the colony, and were seen for 12–14 days until the end of the experiments \((n = 6)\). In contrast, all unfamiliar invaders larger than 10 mm CW were attacked and expelled by the mother or withdrew, mostly within 30 minutes \((n = 10; 10.6–14.2\text{ mm CW})\). Those smaller than 10 mm CW \((n = 4; 7.6–9.6\text{ mm CW})\) were not attacked and expelled. Two of these smaller nonfamiliar C-1 individuals had left the test plant four and five days after introduction and were found dead of desiccation on the laboratory floor.

**Cohort-1 Defense Against Unfamiliar Versus Familiar Crabs**

Do C-1 individuals participate in colony defense? Because of the secretive life of the C-1 individuals within the leaf axils, we could not directly observe their behavior. To determine their role in colony defense, we studied the fate of C-1 individuals after they were released into unfamiliar colonies with only C-1 individuals present.

In February and June 1999, C-1 individuals of 7.2–13.0 mm CW were collected from different bromeliads in the field, individually marked, and released within one hour into a foreign colony \((n = 11\text{ bromeliads})\) or their natal colony \((n = 8\text{ bromeliads})\). From these test colonies, the mother crabs had previously been removed so that the invaders encountered only juveniles and nonreproductive C-1 individuals on the plant. At the start of the experiment, it was not possible to determine the exact number of C-1 individuals in the colony, because this can only be done following dissection of the bromeliad. After seven days, the plants were dissected and the content of the leaf axils was studied.

After seven days, all familiar C-1 individuals that were introduced in their natal colony \((n_{\text{familiar}} = 8)\) were found alive, whereas 73% of the unfamiliar invaders \((n_{\text{unfamiliar}} = 11)\) had disappeared \((\chi^2 = 12.4, df = 1; p = 0.0004)\). Body remains that
were found in two colonies suggest that the colony members
had killed and partly eaten the invaders.

C-1 individuals apparently do not remain in a foreign colony,
irrespective of whether the colony mother was present or only
the C-1 individuals. In some experimental colonies containing
mothers, the colony mother reacted aggressively toward
foreign C-1 individuals, but more frequently, we did not
observe direct aggressive behaviors between any colony
members and the C-1 invader. Our observations suggest that
the C-1 individuals—as well as some of the adult females and
males—that we experimentally introduced into another colony
withdraw on their own. The risk of being injured or killed over
the long term by the colony members appears high for
unfamiliar juveniles and adults from other colonies or
bromeliads.
Alloparental Care

Do the young of the most recent brood benefit from older siblings? In the field, we could not observe the behavior of C-1 toward the C-0 individuals, nor could food availability, predation pressure, or the number of C-1 individuals be manipulated without impairment to the colony. We approached this question by studying the effect of the number and size of C-1 individuals present in a colony on survival and growth of their younger siblings (C-0). Twenty-two colonies with young about two weeks old (C-0) were randomly chosen in the field in May 1997 and May 1998. We counted the C-0 offspring in the nursery axil and recorded the body size (CW) of the breeding female as a correlate of fecundity. The size of the female was also positively related to the size of the bromeliad and the number of leaf axils and thus with the availability of nutritional resources. The mother was removed from each colony to eliminate the strong effects of maternal brood care on C-0 development.

Three C-0 individuals from each colony were taken as a subsample for calculating the total dry mass of the brood (average dry weight of an individual 3 N_{C-0}) at the start of the experiment. After four weeks, the bromeliads were collected and dissected, and the C-0 and C-1 individuals counted and collected. Colonies differed in the number of C-1 crabs, which ranged from 0 to 19. Survival and dry weight increase of the C-0 cohort and the size of the C-1 was measured. The number and size of C-1 individuals present in the colony could not be established at the beginning, but after four weeks when the colonies were dissected, the size and number of C-1 were recorded and the dry mass of the brood was determined (total dry mass of surviving C-0; Sartorius R 160 P balance [Data Weighing Systems, Elk Grove, Ill.], ±0.01 mg accuracy). As a measure of the reproductive success of the colony, we used total dry weight increase of the brood. This was calculated as dry mass of the C-0 young that survived until the end of the experiment minus the estimated dry mass of the brood at start. The value of total dry weight increase is the product of average weight increase of individual young time survival.

This experiment was designed to distinguish between two possible outcomes. First, older sibs could have no or a negative effect on the orphaned brood, for example, when competing for food resources or killing C-0 individuals. In that case, a negative relationship between number of C-1
individuals and the number and growth of the C-0 would be expected. The second possible outcome would be that the older C-1 siblings enhance survival and development of the brood, which may then provide evidence for alloparental care.

The influence of older siblings on growth and survival of the brood was tested with a multiple regression model. Independent variables were the number and average size of C-1 individuals present in the colony, the initial calculated dry mass of the brood, and the size of the colony mother. The size of the mother was positively correlated with fecundity (see Diesel 1992b) and with the number of leaf axes of her plant \( p =0.006, n =97 \), hence with the amount of stored water and food resources. Body size of the mother was therefore used in the model to control for fecundity and food resources. As dependent variable, we used the total dry-weight increase of the brood during the four weeks, as a combined measure of survival and growth of the young.

The results showed that the model was highly significant and explained 70% of the variation in total dry-weight increase of the brood (multiple regression, \( F_{(4,17)}=9.5, r^2 =0.69, p =0.0003 \)). The number of C-1 individuals was the only significant variable in the equation \( t_{(17)}=4.36, p =0.0004 \), whereas the size of mother \( t =1.45, p =0.16 \), the size of the C-0 at start of the experiment \( t =1.53, p =0.14 \), and the size of C-1 individuals \( t =0.63, p =0.54 \) were not significant. That means (p.376)

![Figure 17.4 Positive correlation between number of older siblings (C-1) and estimated total dry-weight increase of the brood.](image)
that the number of older siblings present in a colony explains a very large proportion of the total weight increase of the brood (Fig. 17.4). This means that the more older siblings were present in a colony, the faster the C-0 young grew and the more survived the experiment in absence of the mother.

In this field experiment, the broods (C-0) developed well. Total dry weight of the brood increased even in the absence of their mothers. Thus, reproductive success increased with the number of C-1 siblings present in the colony. At the end of the experiment, the broods were about six weeks old. In absence of the mother, the orphaned C-0 young had left the nursery axil about one to two weeks earlier than usual and spread to other leaf axils of the plant in search of food.

Our results suggest that older siblings enhance survivorship and growth of their younger sibs. The amount of nutritional resources for the development of the brood and the probability that predators are detected and eliminated should increase with the number of defending crabs distributed over the colony. The C-1 individuals may deter and/or kill potential predators such as spiders or increase the availability of food by killing prey and allowing their younger siblings to feed on it. In the laboratory, we observed that C-1 crabs fed with a piece of millipede allowed C-0 individuals to share it. Hence, the activities of C-1 colony members result in nest defense and in exploitation of nutritional resources, which will benefit survival and growth of younger siblings.

The Social System of *Metopaulias depressus*
The results of previous research and the present studies demonstrate that the Jamaican bromeliad crab *Metopaulias depressus* clearly shows traits that are characteristic for small colony eusocial insects and cooperative breeding vertebrates (see Michener 1969, Wilson 1971, Alexander et al. 1991, Crespi 1994, Sherman et al. 1995, Lacey and Sherman 1997, Queller and Strassmann 1998, Choe and Crespi 1997): (1) *Metopaulias depressus* lives in large colonies on bromeliad plants, which provide a supporting microclimate, safety, food, and are expandable and defendable; (2) it has overlapping adult generations; and (3) there are adult but nonreproductive females in the colony together with a single reproductive female, the colony mother. Our new results furthermore suggest that (4) older offspring help in colony defense and have a significant positive impact on the development of their younger siblings.

This highly developed social system is similar to that of cooperatively breeding and eusocial species (Wilson 1971, Sherman et al. 1995) and has not been described for any other crabs. The only crustaceans with a similar social organization so far reported are marine sponge-dwelling alpheid shrimps (Duffy 1996, 2003). In the majority of marine crab species, there is no association between the mother and her offspring after eggs hatch. In many freshwater and fully terrestrial species, in contrast, egg development is direct and the young remain attached to the mother’s body for several days after hatching (Diesel et al. 2000; see also chapter 14). However, no particular brood care or social behaviors had been reported so far.

The basis for the social organization in the bromeliad crabs is that young stay in their natal plant at least for one year, and some may not leave at all. As obligate bromeliad dwellers, their survival depends on regular access to water. When leaving and searching for another bromeliad, they face a high risk of desiccation in the usually dry surrounding habitat. The mortality risk decreases with size: the larger the crab, the higher the chance of surviving dispersal. Experiments with juveniles of the closely related *Sesarma jarvisi* Rathbun 1914 showed a strong positive correlation between body size and resistance to desiccation (Bäurle 1995). An additional size-dependent mortality risk is predation during dispersal (e.g., by spiders, see Diesel 1989) and a high risk of injury or death when entering an occupied bromeliad. On the other side, there
is relative safety in the home plant. Hence, it should be beneficial for C-1 individuals to delay dispersal until they have reached a larger body size.

Young females need to disperse if they want to colonize a new bromeliad for breeding. However, the limited availability of noninhabited, colonizable high-quality plants appears to be a constraint on successful dispersal and colony foundation. For a young female dispersing from the natal colony, the chance to acquire a suitable bromeliad from a usually much larger territory owner is very low. Most of the dispersing females have to find vacant bromeliads, and these are extremely rare. The prospects of successful colony founding in such bromeliads are low and costly, because they are usually filled with leaf litter and because physicochemical conditions are adverse (Diesel 1992a, Diesel and Schuh 1993). It is difficult for a young, relatively small female to clean the leaf axils of leaf litter and to prepare a supporting microclimate in the nursery axil for the brood.

The Lucky Princess
Some colonies held two adult females: the large colony mother and a small subordinate female. These subordinate females were physically able to reproduce (they had passed the “molt of puberty”; see Hartnoll 1964) but never carried eggs. At the same time, other females of the same size take the risk of dispersal and become solitary breeding foundresses.

What could be the benefits in staying home? Subordinate females may gain some inclusive fitness benefits by exerting altruistic behavior and improving survival and growth of younger siblings. However, this component of inclusive fitness may be negligible compared to the gain in direct fitness from increased survival and future reproductive success (see Clutton-Brock 2002) when taking over the bromeliad location (present plant or subsequently appearing shoots) once the colony mother dies (see Emlen 1991).

Marking experiments to follow the fate of subordinate females in the field over one year were not successful, because they are difficult to locate without destroying the bromeliad. Observations on marked bromeliads with colonies, however, suggest that primiparous females took over a nest location with young crabs after the colony mother died.
Subordinate females possibly refrain from early dispersal and reproduction for the benefit of staying at home and taking over the colony, or acquiring a new, adjacent bromeliad clone. This is supported by the observations that several old rhizomes repeatedly produced large plants that served as new nest locations and were perpetually occupied by colonies for the last 14 years. Younger females accompanied by smaller conspecifics usually inhabited the new clones. We assume that most of these females are subordinates of the former colony, now in charge of her siblings. However, the exact degree of relatedness still needs to be clarified with genetic methods.

Why Defend the Home Bromeliad?
Among the possible conspecific invaders, adult females can inflict the highest costs to the resident female. Adult females seeking a suitable new breeding site because their home plant has been destroyed may evict the resident females from their home plant. In our experiment, however, colony mothers attacked and always expelled intruding adult females even if they were considerably larger. Fights among females were more vigorous than those involving females versus males. On the other hand, breeding females often tolerated adult female colony members, presumably their daughters. Males, too, were attacked and evicted from the colony. In the field, however, we occasionally observed males that spent a few days in a colony.

Colony mothers also behaved aggressively against C-1 individuals from other colonies if their size was at least 10 mm CW, but did not respond toward smaller nonfamiliar individuals. How and why do resident females distinguish between nonfamiliar larger and smaller C-1 individuals? It may reflect the situation in nature, where C-1 crabs disperse from the colony at about 9 mm CW and thus only juveniles of this size and larger may become potential invaders and be recognized as such by the resident female.

The senior author of this paper made a similar observation in an earlier experiment (R. Diesel, unpublished data), in which he exchanged the larvae between nurseries from different bromeliad crab colonies. Females did accept the unrelated offspring and continued with brood care. A similar behavior is reported from burrow-living crayfish. Figler et al. (1997)
observed that females did not discriminate between their own and unrelated early offspring.

By defending the plant against unrelated females, the owner eliminates the risk of investing in nonrelated young. Therefore, selection for recognition of a female’s own brood is not expected as long as the offspring are small. This lack of recognition of early juveniles, however, may be a cause for evolution of alternative strategies such as brood parasitism. Preliminary molecular results based on microsatellite and mitochondrial data suggest that occasionally some individuals of the C-0 cohort in a colony may not be direct descendents of the colony mother, and thus larvae dumping by other females may occur (L. Heine, C.D. Schubart, I. Marcade, M. Klinkicht, and R. Diesel, unpublished results).

Alloparental Care

Alloparental care is one of the most prevalent cooperative tasks in social species (see Emlen 1991). Our experiments suggest that older siblings support growth and survival of their younger siblings. The behaviors of C-1 individuals responsible for this result are not known. Older siblings may increase food availability and decrease predation risk for the C-0. These activities may not be costly to the C-1 individuals but could simply be a byproduct of their normal behavior.

Social Evolution in Other Crustaceans

The documentation of the social breeding system in *Metopaulias depressus* leads to the question why similar helper systems did not evolve in the other Jamaican terrestrial crabs. One of the most important predispositions for the evolution of sociality is extended parental care. This cannot evolve in species with dispersing planktonic larvae, but species with direct development have the preconditions to evolve extended parental care (Diesel et al. 2000, Thiel 2003). This is the common reproductive mode of freshwater and terrestrial crabs throughout the world. The Jamaican endemic species of the genus *Sesarma* (closest relatives of *M. depressus*) are a rare exception in still showing an abbreviated larval development, but with the important difference of larval retention in the parental habitat. In most species for which breeding is known (*S. fossarum*, *S. windsor*, *S. ayatum*, *S. verleyi*, *S. jarvisi*, see Diesel et al. 2000; R. Diesel, unpublished observations), the larvae develop in confined, nonexpandable
microhabitats such as rock pools, burrows, and snail shells. With the exception of the snail shell crab *S. jarvisi* (see below), there is so far no evidence that extended parental care occurs in these species (of the John Crow mountain crab *S. cookie*, the breeding habitat is still unknown). Only cohorts of larvae were found, and juveniles appear to disperse shortly after metamorphosis.

The only other Jamaican crab with known social behavior is the snail shell crab *Sesarma jarvisi*, which has reached the highest social level next to the bromeliad crab. This crab lives in the mountain rain forests of central Jamaica. The mother selects empty shells of large land snails for breeding (Diesel and Horst 1995, Bäurle 1995). She prepares the shell for breeding and collects about 5 milliliters of dew water in the shell. The few larvae are released into the miniature aquarium and develop rapidly into juveniles. The mother cares for the larvae and juveniles in the snail shell for months, protecting them from predators, providing food, and maintaining a supporting microclimate. Although this breeding habitat provides a suitable environment for the young and is well defendable, it lacks nutritional resources, is found in higher densities, and is used only once for raising young. After about three months, too much detritus has accumulated in the shell and the juveniles have grown to a size that space in the shell becomes limited, so the juveniles have to disperse. Hence, there is no opportunity for helping and later takeover, since the breeding habitat loses its value during the rearing of a single brood.

Breeding habitats of most other Jamaican crabs are thus either too small or ephemeral or do not contain food. In contrast, the bromeliads are large, stable, and renewable habitats that also provide food. This was probably the major key difference that promoted the social evolution of the bromeliad crab.

Little is known about the breeding behavior of other true freshwater and terrestrial crab species. However, there may be other breeding habitats favoring extended parental care. We predict that species that breed in tree holes or phytotelmata are good candidates for extended brood care. These are such species as the East African Usambara tree-hole crab, *Potamonautes raybouldi* (Potamonautidae), from Kenya and Tanzania, which rears its young in water-filled tree holes (Bayliss 2002, Cumberlidge and Vannini 2004). A similar brood
care pattern may be found in the tree-hole crabs of West Africa, Madagascar, and Southeast Asia (see Cumberlidge et al. 2005), but the evolution of cooperative breeding in these cases is unlikely because of the limited size of their breeding territory and the lack of nutritional resources. Some burrowing species in particularly harsh habitats should also be candidates for extended parental care (for burrowing crayfish, see chapter 15). Considering the large number and diversity of true freshwater and terrestrial crab species in the world, their mostly concealed way of life, and our present poor knowledge about their biology, many interesting discoveries of social behavior in crabs may still await us.

With their direct development, freshwater crabs have one important predisposition to evolve extended parental care, but their breeding habitats are probably too confined or too ephemeral to evolve this pattern. In comparison, bromeliads are stable habitats with renewable resources. Comparative studies between tree-hole crabs and the bromeliad crab could help us to understand the role of the microhabitat in the evolution of extended parental care and advanced social systems.

Spanier et al. (1993) asked, “Why are there no reports of eusocial marine crustaceans?” They argued that several characteristics occasionally found in crustaceans, such as cavity nesting, overlapping generations, restricted dispersal, and some form of parental care, would favor eusociality according to Alexander et al. (1991). As shown in this study, one should expand the question to include land-living crustaceans, as well. Also, Duffy (2003) agrees that “among the Crustacea there are many taxa that meet one or more of Crespi’s criteria but few that meet all of them.” For example, crustaceans thriving on corals can rely on a long-lived habitat providing shelter and food. However, they reproduce by planktonic larvae, probably because corals are not patchy enough to favor juvenile retention in the adult habitat.

Planktonic dispersal thus acts against the evolution of extended parental care in marine crustaceans. This conjecture is supported by the occurrence of extended parental care, or other family group formation, in direct-developing amphipods living in family groups in sponges or ascidians (see Thiel 2000) and sponge-inhabiting shrimps of the genus Synalpheus (see Duffy 1996). Duffy (1996, 2003; see also chapter 18) showed
that some of these species show a high degree of sociality and suggested that the evolution of eusociality has been favored by the presence of four characteristics that are shared with many social insects (see also Crespi 1994): (1) direct development; resulting in kin association; (2) ecological specialization on a valuable, long-lived resource; (3) strong competition for the host resource; and (4) possession of weaponry effective in monopolizing it. Our present study on the bromeliad crab *Metopaulias depressus* shows that a similar social evolution occurred in a terrestrial environment and even with a larval development through swimming stages.

Offspring retained in a confined nestlike structure usually have limited access to food. Therefore, various species of invertebrates and vertebrates provide their eggs or embryos with nutritional resources as yolk (lecitotrophic eggs). In addition, some have evolved an active food-provisioning behavior by the parents. For example, in the desert isopod *Hemilepistus reaumuri*, the young remain in a burrow without food resources. Both parents forage for food away from the offspring nest, carry food back to the nest, and provision the offspring (Linsenmair 1972; see also chapter 16). A similar food-provisioning social behavior is well known in many social insects (Wilson 1971) and also occurs in the ambrosia beetle *Austroplatypus incompertus* (see Kent and Simpson 1992) and some passalid beetles (see Schuster and Schuster 1996).

An interesting parallel to the bromeliad crab is found in frogs. The Jamaican bromeliad frogs (*Osteopilus brunneus*) deposit their eggs in the same bromeliad species as the bromeliad crab (avoiding plants with crabs). The tadpoles develop in the leaf axils with very limited nutritional resources and are fed by their mother with unfertilized eggs (Lannoo et al. 1987). Similar provisioning of fertilized or unfertilized eggs to oophagous tadpoles also evolved in other frog species that use water-filled bromeliad axils, tree holes, or bamboo stumps to deposit their larvae (Weygoldt 1980, Brust 1993, Caldwell and Oliveira 1999, Kam et al. 2000). Food provisioning in frogs frequently involves eggs. They seem to be a more convenient and handy food item to feed the young, than carrying small prey items. This early cannibalism may not be a useful predisposition for social evolution, though.

Future Directions
Despite many years of research on the bromeliad crab, interesting questions remain to be studied in order to understand the social organization of the crab. A better understanding of the forces selecting for the social organization of the bromeliad crab should provide valuable information for understanding the evolution of higher social systems in other animal taxa.
The Mating System and Genetic Relatedness of the Colony Members

Most important for understanding the social organization of the bromeliad crab will be knowledge of the genetic relationships among the colony members. Are the individuals of the C-0 or the C-1 cohorts full or half-siblings? Is the subordinate female the daughter of the colony mother? The genetic relatedness is predicted to affect their social behavior. If, for example, older offspring have different fathers, then the young siblings are half-siblings. Is this degree of relatedness high enough for alloparental care behavior to evolve? Would a subordinate daughter help raise additional competitors with a low degree of relatedness?

Whether offspring clutches of the bromeliad crab have one or multiple fathers depends on the mating system. With the new marking, tracking, and observation techniques available today, it would be interesting to study the mating behavior of the bromeliad crab. Presently, only a few basic details on mating behavior are known (R. Diesel, unpublished observations): males usually leave their home plant during the mating season in the Cockpit Country (December and January) and visit and mate with surrounding females. They may move from bromeliad to bromeliad and return to their home plant or spend a few days on the bromeliad with the female. Visits on a bromeliad with a colony mother might be dangerous for a male, especially if the female is its size or larger. As shown in the defense experiments reported above, females do attack males and could injure or even kill a male with their strong and piercing claws (in one case we observed that a female had killed a male in the field). Two sensory cues may be important for males during mating. (1) We have observed that when the male enters a bromeliad, he sometimes employs a short series of taps with the points of his claws on the surface of the leaf (claw drumming on the bromeliad leaf). This possible courtship signal will travel over the plant and tell the female that there is a visitor and might reduce aggressive interactions between the prospective mates. (2) By sampling the axil water with the claw (see below), males could probably obtain information on the receptive state of the female.

An important determinant of paternity is the mating behavior of the female. Does she mate with different males within a mating season and over successive mating seasons? If so, how does she use the sperm of these males for fertilization?

(p.382)
Preliminary molecular results suggest that multiple paternity is reflected within single cohorts (L. Heine, J. Heinze, C.D. Schubart, unpublished results). What is the consequent degree of relatedness among the colony members? If it is low, one has to address the question why would they still cooperate. The senior author has observed different males visiting a female, but it is not known whether multiple mating took place in these cases. There is a high chance that a female is mating repeatedly with the same male even over successive mating seasons, because males live stationary in an area and appear to have a defined home range with several females, similar to those of the marine spider crab *Inachus phalangium* (see Diesel 1986). Females store the sperm in seminal receptacles for long periods. Several females dissected six months after the mating and spawning season held large sperm reserves (R. Diesel, unpublished data). Thus, the sperm of one male may be used repeatedly. However, the influence of sperm competition is still unknown. Females may be able to manipulate the degree of genetic relatedness among the offspring by selective mating or selective sperm use.

The study of the degree of relatedness among the colony members would provide valuable information not only for the interpretation of the behavior of C-1 individuals in respect to alloparental care but also for the recognition of colony members, thereby helping to understand the evolution of the social system of the bromeliad crab.
Larva Dumping

An additional possibility for a lower degree of relatedness among the colony members would be through individuals that came from outside the colony. Preliminary studies with microsatellite and mtDNA markers showed that some colonies included small C-0 individuals that did not share alleles or haplotypes with the colony mother (L. Heine, C.D. Schubart, I. Marcade, M. Klinkicht, and R. Diesel, unpublished results).

(p.383) How do these crabs come into the colony? Small juveniles of this size (about 3 mm CW) could not have invaded the colony from another bromeliad. The most likely explanation is that “larvae dumping” occurs in the bromeliad crab. Females with eggs ready to hatch may search for colonies with larvae and release some of their own larvae into the nursery while the colony mother is somewhere else on the plant. This could be an interesting alternative strategy for females that do not possess a suitable bromeliad for breeding or are yet too small and ineffective to prepare and maintain a nursery axil. Apparently, females cannot or do not discriminate between their own versus unrelated larvae. In one experiment where larvae were swapped between two colonies, both mothers continued to care for the foster larvae (R. Diesel, unpublished observations). With molecular techniques, it will be possible to establish how frequently unrelated C-0 individuals occur, and additional field observations are necessary to explain how these get into the nursery and which females are releasing them.
Recognition of Nest Mates

How do bromeliad crabs recognize an individual as familiar, unfamiliar, colony member, or possibly kin? The mechanisms underlying the recognition should be studied. We suggest that relevant cues may be water-soluble components. We frequently observed that crabs use the tips of their chelae and mouthparts to “sample” the axil water or the moist body surface of another crab. Crabs that were released on an unfamiliar bromeliad, for example, walk down the leaf to the water edge, sample the water with one claw, and move the tip of the chela to the mouthparts in a “drinking” manner. They may gain information on the reproductive state of a female and whether the bromeliad or axil is familiar or unfamiliar. The latter could explain that in the experiments on colony defense, some individuals released into an unfamiliar colony left the bromeliad on their own. Is there a “colony odor”? Do genetically related individuals produce similar odors, or excretions or do miniature ecosystems have distinct bouquets because of their different microbe assembly and thus the crabs on a bromeliad collectively achieve specific “colony odor”?

The Lucky Princess

What is the fate of an adult subordinate female? The reproductive success of dispersing primiparous females and the subordinate females that remain in their home plant should be compared. Does it pay to remain home and forfeit reproduction for the prospect of inheriting the nest location? In this system, the daughter not only may inherit directly the mother’s territory but also could await a new territory that develops at the same location in a very predictable way in form of a lateral shoot. Hence, bromeliads are like territories with renewable resources. To understand this unique system, future research should include the bromeliad dynamics.
Summary

The Jamaican bromeliad crab *Metopaulias depressus* (Decapoda, Brachyura, Sesarmidae) lives exclusively in the water-storing leaf axils of bromeliad plants, which provide a supporting microclimate, safety, and food and are expandable and defendable resources. (p.384) We suggest that the species evolved extended parental care to ensure reproduction in this scattered microhabitat. Theory and comparison with other social animals predict that such limited habitat availability may predispose species for the evolution of eusociality, which is classically characterized by overlapping adult generations, reproductive division of labor (caste formation), and altruistic behavior by nonreproductives. In this study, we show that similar characteristics are found in the bromeliad crab: it lives in large colonies consisting of the colony mother and her offspring. Only the colony mother produces eggs. More than 80% of the colonies consisted of at least two annual broods, and 21.5% of the colonies held at least one additional adult crab besides the colony mother. Hence, some offspring remain in the natal colony until they become adult and thus form overlapping generations. Young adult females stayed in their natal colony as subordinate females and forfeited reproduction in the presence of the colony mother, while others of the same age cohort dispersed to other bromeliads (foundresses) and produced eggs. Colony members defended the bromeliad territory against unfamiliar invaders. The colony mother vigorously fought off unfamiliar adult females. Individuals of the C-1 cohort and the colony mother repelled unfamiliar C-1 invaders but not familiar C-1 individuals used as controls. The results of a field experiment in which the colony mother was removed showed that the C-0 broods benefit from the presence of older siblings. That is, C-1 offspring that are at least one year old or nonreproductive adults participate in colony defense and increase survival and growth of their younger siblings. Thus, the bromeliad crab has evolved traits that are characteristic of eusocial and cooperatively breeding species. It displays a high degree of sociality that is unique among crabs and represents the pinnacle of a remarkable and swift social evolution from a nonsocial marine ancestor.

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The Social Breeding System of the Jamaican Bromeliad Crab Metopaulias depressus

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