The Mating System of Symbiotic Crustaceans

A Conceptual Model Based on Optimality and Ecological Constraints

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Abstract and Keywords

This chapter proposes a conceptual model predicting the mating system of symbiotic crustaceans. It assumes that males and females have different optimal mating strategies which they attempt to attain by defending and moving between hosts, and that host characteristics and predation risk limit the behavioral options of symbiotic individuals. Five mating systems are predicted: (i) monogamy when predation risk is high, hosts are scarce, morphologically simple, and small in size; (ii) host-defense polygyny when predation risk is high, hosts are scarce, simple, and intermediate in size; (iii) pure-search polygynandry of mobile females when predation risk is low, hosts are abundant, complex, and large; (iv) pure-search polygynandry of sedentary females when predation risk is moderate to high, hosts are scarce, and extremely small; and
(v) female-centered polygyny when predation risk is moderate, hosts are neither abundant nor scarce, and intermediate in size. Empirical evidence supports the model's predictions.

**Keywords:** symbiosis, host abundance, morphology, defense, predation risk, mating systems

(p.250) During the last decades, several conceptual, graphical, and mathematical models have been proposed to explain particular or more general aspects of the breeding ecology of both marine and terrestrial organisms (e.g., Parker 1970, Jarman 1974, Bradbury and Vehrencamp 1977, Wickler and Seibt 1981, Grafen and Ridley 1983). The pioneering and influential work by Emlen and Oring (1977), and most recently that of Shuster and Wade (2003), are among the most comprehensive contributions. Most models predict particular mating systems depending on a limited set of ecological conditions, mostly the abundance and distribution of resources and receptive females in space and time, which ultimately determines the “environmental potential for polygamy” (Emlen and Oring 1977). Also, Shuster and Wade (2003) have recently proposed a method for quantifying the source and intensity of selection with which to improve our understanding about the evolution of mating systems.

Among marine crustaceans, mating systems are diverse (see reviews on hermit crabs, Hazlett 1975; brachyuran crabs, Christy 1987; caridean shrimps, Correa and Thiel 2003; isopods and amphipods, Jormalainen 1998), and several studies have attempted to identify the factors determining their mating systems (i.e., Christy 1987, Correa and Thiel 2003, Bauer 2004). Experimental and descriptive studies of crustaceans have largely corroborated Emlen and Oring's model but have also drawn attention to the importance of additional factors such as sperm competition (Parker 1970) and pre- and postcopulatory mate choice (Eberhard 1996) in
shaping mating strategies. Although our understanding of mating behaviors in several groups of crustaceans has improved, no study so far has attempted to explain the variety of mating systems of symbiotic crustaceans. There is also increasing appreciation that environmental factors, such as habitat characteristics, exert an influence on mating systems (Knowlton 1980, Thiel and Baeza 2001). Promising taxa in which to explore the effects of the environment are those inhabiting well-defined microenvironments, namely, species that have assumed a symbiotic lifestyle.

Figure 12.1 (A) The porcelain crab *Allopetrolisthes spinifrons* that dwells solitarily on the column and occasionally among the tentacles of its host, the sea anemone *Phymactis papillosa* (=*clematis*) in intertidal coastal waters of Chile. (B) The porcelain crab *Liopetrolisthes mitra* that lives in unstructured multi-individual aggregations among the spines and beneath the oral disk of its host, the sea urchin *Tetrapygus niger* in subtidal coastal waters of Chile.
Crustaceans are among the most diverse marine invertebrates, and many (including some isopods, amphipods, shrimps, crabs) have developed complex interrelations with other marine invertebrates from many different taxa (i.e., sponges, sea anemones, corals, among others) (Ross 1983, Thiel and Baeza 2001). These hosts differ widely in body plan, size, morphology, and general ecology (i.e., abundance, dispersion pattern) (Thiel and Baeza 2001, Baeza and Thiel 2003). In turn, symbiotic crustaceans feature a wide array of population or deme structures on their hosts (Thiel and Baeza 2001). Some dwell in/on hosts as solitary individuals (Diesel 1986; Fig. 12.1A), some are found as heterosexual pairs (Knowlton 1980), and others as dense unstructured aggregations of individuals (Baeza and Thiel 2000; Fig. 12.1B). The wide range of hosts used by symbiotic crustaceans and the diversity of their population or deme structures represent an opportunity to explore and understand those environmental conditions constraining or promoting particular mating associations in marine and terrestrial organisms exploiting small discontinuous habitats (including parasitoid insects, parasite helminthes).

Our aim in this chapter is to propose and evaluate a conceptual model that predicts the mating system of symbiotic crustaceans depending on particular host characteristics and environmental conditions (e.g., predation pressure).

Model Structure and Assumptions
Our model assumes that males and females have different optimal mating strategies, which they attempt to realize by defending (i.e., host guarding) and moving (host switching) between hosts, and that the environment limits the behavioral options of symbiotic individuals.

Different Optimal Mating Strategies of the Sexes
We assume that polygyny is the optimal male mating strategy whereas monogamy coupled with mate choice is the optimal female mating strategy (Emlen and Oring 1977). Males are usually considered as “eager” to mate because their fitness is maximized by reproducing with as many females as possible. In contrast, females are perceived as “reluctant” to mate because their reproductive potential is lower and fitness is generally maximized by choosing a male of “high quality” (but see chapter 2). Females may obtain direct nongenetic benefits (i.e., resources, parental care) or indirect genetic benefits (i.e.,
“good genes”; Hunt et al. 2004) by choosing particular males. In species where females obtain only sperm from males, such as in most marine crustaceans with dispersing larvae, females are thought to derive indirect genetic benefits (good genes) by choosing a male of high quality because offspring inherit both the genes underlying choice and the genes for quality (Hunt et al. 2004). In turn, direct nongenetic benefits such as food, protection against natural enemies, and a dwelling in which to brood their embryos may also be important for females. Because of the close interdependence between symbionts and their hosts, these direct benefits may more often outweigh genetic benefits in symbiotic crustaceans than in free-living species. Overall, this perception about the different optimal mating strategies of males and females is based on classical sexual selection and parental investment theories (Darwin 1871, Bateman 1948, Trivers 1972) and still constitutes the classic Darwinian paradigm on which most theoretical models about the evolution of animal breeding systems are based.

(p.253) Host Guarding and Host Switching

The host organism constitutes a critical resource for a symbiotic organism. Males may increase their chances to mate by monopolizing hosts or by roaming among them if these harbor females. Similarly, females may be able to choose among mates only if they are capable of visiting hosts harboring males of dissimilar quality. Host guarding is any activity performed to secure a particular host against intruders (see Wilson 1975). Host switching is the movement of individuals among hosts. These are completely different behavioral traits. For instance, a symbiont may change hosts frequently and exclude all other conspecifics each time it occupies a new host or may be sedentary and share space on the host. Resource defense and site tenacity have been recognized previously as important elements in crustacean mating behavior (e.g., Christy 1987; see also chapter 10). For instance, males of the shrimp Alpheus armatus have been shown to increase their reproductive success by increasing the rate of host switching, which in turn provides more opportunities to find receptive females (Knowlton 1980). Similarly, monopolization of hosts allows males of symbiotic species to defend their refuges and potential mating partners on them (Nakashima 1987). Thus, we expect both host guarding and host switching to have important effects on
individual reproductive success because both behaviors affect the rate and number of interactions between potential mates.

Environmental Constraints

Emlen and Oring (1977) considered the temporal and spatial distribution of receptive females as important elements shaping mating systems. We also consider the spatial distribution of receptive females as of primary importance, but we focus on host characteristics because we believe they ultimately control female abundance and distribution in symbiotic organisms. Three host characteristics—relative size, abundance, and morphological complexity—together with predation risk, are proposed as primary ecological factors affecting host guarding and host switching (Fig. 12.2). These host characteristics were chosen based on our review of effects of ecological factors on intraspecific associations in symbiotic crustaceans. For instance, the hosts of solitary symbiotic crustaceans are, on average, smaller and less abundant and have simpler morphological complexity than the hosts of crustaceans that live in large unstructured groups (Thiel and Baeza 2001, Baeza and Thiel 2003). Predation is known to affect many reproductive traits of marine crustaceans, including mate-searching behavior (chapter 10). Therefore, we expect that predation risk, host size, abundance, and morphological complexity will have important effects on both host guarding and host switching, ultimately determining the rate and number of interactions between potential competitors and mates.

The Optimality Approach

We assume that individuals attempt to respond “optimally” to their environment (Maynard-Smith 1978). This optimal response by symbionts is determined by costs and benefits associated with specific behaviors (i.e., host guarding and host switching) that vary with particular environmental conditions (i.e., host size, abundance, morphological complexity, predation risk). The optimal behavior of symbionts is that (p. 254)
where the net benefit or the benefit-to-cost ratio is the largest under prevailing conditions (Maynard-Smith 1978). Increases in survivorship, growth, or ultimately, mating opportunities are potential benefits of host guarding and host switching. In turn, the amount of energy an individual must expend on resource-guarding activities and the risks of falling victim to predators when away from hosts are potential costs. These benefits and costs ultimately influence lifetime reproductive success, the currency being optimized in this model.

By following this optimality approach, we make the following predictions. All else being equal, with increasing host abundance, the probability of symbionts monopolizing hosts should decrease, while the probability of symbionts moving among host individuals (i.e., host switching) should increase. This is because increased host abundance decreases the benefits of monopolizing hosts and the costs of roaming around them. Second, with increasing morphological complexity, the probability of symbionts monopolizing hosts should decrease, while the probability of movement among hosts should remain constant. This is because the host’s morphological complexity renders host guarding too costly but

Figure 12.2 Proposed model of mating systems of symbiotic crustaceans. Risk of predation and host characteristics (i.e., relative size, abundance, morphological complexity) constrain and/or promote host monopolization and host switching, behavioral traits used by individuals to achieve their optimal mating strategy. The decision whether or not to guard and roam among individual hosts is an optimality problem crucial in determining the behavioral strategies of both males and females and therefore the mating system of symbiotic crustaceans.
affects neither the cost nor the benefits of roaming among them. Third, increasing host size (relative to symbiont size) should not affect the frequency of movements among hosts (i.e., host switching), but should decrease host guarding. This is because neither the costs nor the benefits of roaming among hosts change with host relative body size, but increases in host relative body size should render host monopolization by symbionts too costly. Finally, with increasing predation pressure, host guarding should increase but host switching should decrease. This is because the host's value in offering protection against predators increases with predation risk but renders movements among hosts more risky (Fig. 12.3).

**Sexual Dimorphism and Alternative Mating Tactics**

Theory predicts that intrasexual selection favors weapons (i.e., chelae, gnathopods, and maxillipeds in crustaceans) or other traits (e.g., large body size) that improve the potential of males to monopolize females. In turn, intersexual selection promotes ornaments in males that increase their chance to be chosen by and mate with females (Darwin 1871). Both intra- and intersexual selection, together with the action of natural selection (e.g., fecundity selection on females, cost of ornaments in terms of growth and survival on males), should ultimately determine how different in terms of morphology, coloration, and/or behavior males should be from females. Sexual selection theory also predicts that intense intrasexual selection favors alternative reproductive tactics in subdominant males (e.g., sneaking or sex change; Andersson 1994). The consequences in terms of sexual
dimorphism and alternative mating tactics for symbionts adopting a particular mating system are discussed below.

Mating Systems
We propose five mating system categories that should occur in particular environments, and we discuss the behavioral tactics adopted by individuals for each. These mating categories are named in terms of number and variability of copulations experienced by both males and females (sensu Shuster and Wade 2003). Thus, monogamy refers to the mating system in which both males and females have a single mate for life. In polygyny, females mate with a single male in their lives, but males may mate with more than one female. Polygynandry occurs when both sexes are variable in their mate numbers, but males are more variable than females (see Shuster and Wade 2003). Herein, we distinguish two categories of polygyny and two categories of polygynandry. These mating categories are envisioned as occurring within a three-dimensional space resulting from the interaction among predation risk, host relative size/host complexity, and host abundance (Fig. 12.4, Table 12.1). Even though
Table 12.1. The five mating system categories occurring in symbiotic crustaceans proposed in the present model.

Figure 12.4 Mating systems predicted for symbiotic crustaceans according to a specific set of environmental conditions. The interaction among predation risk, host relative size, and abundance is envisioned as a three-dimensional space in which different mating systems occur. x and y, number of males (M) and females (F), respectively, found in a host under the different mating systems.
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<td><em>Periclimenes ornatus</em> (Omori et al. 1994)</td>
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### Mating System and Selected Examples

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Environmental conditions determining each mating system, the intensity of sexual selection, and consequences in terms of sexual dimorphism and the presence of alternative mating tactics are shown. Selected empirical examples supporting the proposed model in each mating system category are listed. Additional studies may be found in Thiel and Baeza (2001).

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<td>Sexual selection intensity&lt;sup&gt;e&lt;/sup&gt;</td>
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(Yanagisawa and Hamaishi 1986)

5. Female-guarding polygyny

*Inachus phalangium* (Diesel 1986)

*Athanas kominatoensis* (Nakashima 1987)

Environmental conditions determining each mating system, the intensity of sexual selection, and consequences in terms of sexual dimorphism and the presence of alternative mating tactics are shown. Selected empirical examples supporting the proposed model in each mating system category are listed. Additional studies may be found in Thiel and Baeza (2001).

<sup>a</sup>S, small; M, intermediate; L, large.

<sup>b</sup>S, simple; M, moderate; L, complex.

<sup>c</sup>S, scarce; M, intermediate; L, abundant.
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dS, low; M, moderate; L, high.

eS, low; M, moderate; L, high.

fM, male; F, female.

gY, yes; N, no.

hAdditional information on the mating behavior and reproductive biology of this species is required.
These mating systems are introduced as discrete categories, they are better considered “variations of a single theme.” After introducing each mating category, examples that support the predictions of this model are discussed.
Monogamy

Monogamy should evolve when hosts are morphologically simple, small enough to support few individuals, and relatively rare and when predation risk away from hosts is high. Under these circumstances, movements among hosts are severely constrained. Host guarding is favored in males and females due to host scarcity and because of the host’s value in offering protection against predators. The small body size of hosts makes it possible for individuals to monopolize the host by guarding. Small host body size and scarcity also result in females not being clumped on a single host, but rather distributed more uniformly among them. It is therefore difficult either for a male to monopolize more than a single female at the same time on the same host or to visit additional females on different hosts. Because spatial constraints allow only few adult symbiotic individuals to cohabit on the same host, both males and females maximize their reproductive success by sharing “their” dwelling with a member of the opposite sex during their lifetime.

Temporal synchrony of receptivity among females should reinforce this mating system while low synchrony should provide an opportunity for males to seek extrapair copulations. No or low sexual dimorphism in body size and weaponry is expected due to the low intensity of sexual selection in this mating system (i.e., low variance in mating success among both males and females) (see Shuster and Wade 2003) (Table 12.1). However, if these monogamous species experience food limitation, natural selection might favor sexual dimorphism in body size. Small body size in males could be favored because that would make more food available for their female partners for offspring production (i.e., a form of indirect paternal care; Andersson 1994, Shuster and Wade 2003). As a result, monogamous symbiotic crustaceans with a limited food supply (e.g., parasites) should feature monogamy characterized by dwarf males.

In agreement with our prediction, many species of symbiotic shrimps, crabs, and isopods have been reported living in male-female pairs, in relatively small and scarce hosts inhabiting tropical environments where predation risk off hosts is presumed to be high (see references in Thiel and Baeza 2001). A monogamous mating system with reduced or no dimorphism in body size has been confirmed in at least two of these species (*Alpheus immaculatus*, Knowlton 1980, Knowlton and...
Keller 1983; *Periclimenes ornatus*, Omori et al. 1994). In other monogamous species that live trapped within host body cavities and that strongly depend on their hosts for—most probably—limited food (e.g., a parasitic pinnotherid crab *Pinnotheres halingi*, Hamel et al. 1999), males are dwarfs, in agreement with the prediction from this model.

**Host-Defense Polygyny**

Host-defense polygyny should evolve when hosts are morphologically simple, of a size that supports more than two but not too many symbiotic individuals, and are relatively rare and when predation risk off hosts is high or moderate. Under these circumstances, movement among hosts is constrained, but their intermediate (p.259) carrying capacity and morphological simplicity allow males to defend relatively stable aggregations of females and to efficiently exclude intruders of the same sex. That is, males have the opportunity to mate with more than a single female in a short period of time in or on a guarded host. Host guarding by males is favored because of host scarcity and high predation risk and is further enforced by the clumped distribution of females. Thus, one should expect a correlation between host size, male size, and the number of females per host, with large hosts harboring large males and numerous females and small hosts harboring small males and few females. While males are predicted to maximize their reproductive success by monopolizing host individuals and reproducing with all females present on “their” hosts, females may select large hosts guarded by large “high-quality” males in order to increase their fitness under either a “good genes” of direct-benefits scenario.

Breeding asynchrony of females should reinforce this mating pattern, but synchrony of female receptivity should make this mating system drift toward pure-search polygynandry (see below). Because males defend hosts, sexual dimorphism in body size and in structures potentially usable as weapons (chelae, gnathopods, and/or maxillipeds) should be favored by intrasexual competition. Female mate choice may additionally select for male ornaments (e.g., colorful stripes). Alternative mating tactics such as sneaking, satellite, and/or female-mimicking males could be expected in species featuring host-
defense polygyny because host characteristics and predation risk promote variance in mating success among males.

Species featuring host-defense polygyny include the ascidian-dwelling amphipod *Anamixis hanseni* (Thomas and Barnard 1983) and the sponge-dwelling isopod *Paracerceis sculpta* (Shuster and Wade 1991). In these species, a single male guards (the entrance of) a relatively large host that allows the cohabitation of several females. In *P. sculpta*, information on temporal and spatial receptivity of females and on male and female reproductive behavior and sexual dimorphism is extensive. The dominant males (alpha males) are larger than females and female receptive synchrony is relatively low, supporting our predictions (Shuster and Wade 2003). However, information on host abundance and predation risk is lacking in both species. Also in *P. sculpta*, three genetically determined male morphs featuring dissimilar mating strategies coexist in the same population (Shuster and Wade 1991), supporting our prediction.

**Female-Centered Polygyny**

Female-centered polygyny should evolve when host body size supports a moderate number of symbiotic individuals at the same time and when host abundance and predation pressure are moderate. This combination of factors imposes constraints (albeit not severe) on host switching. Host guarding is constrained due to the morphological complexity and intermediate body size of hosts and the consequent high costs of defense. Under these circumstances, females should be randomly distributed among hosts, and at moderate densities. As a result of the moderate abundance of females within and among hosts and their dispersion pattern, guarding of females by males becomes more profitable than host guarding or pure-searching strategies (see below). Males are expected to roam within hosts and among hosts (when possible) in search of receptive females. When females are found, males should guard and protect them against other males until they become receptive, at which time they should be mated. (p.260) After mating, males should leave females in search of additional females in the same or other hosts. Females may resist copulations, and even select high-quality males, to increase their reproductive success under a good-genes scenario.
because moderate predation risk allows at least some host-switching behavior.

Breeding asynchrony should reinforce this mating pattern because it allows males to search, find, guard, and mate multiple females in sequence. On the other hand, if females become receptive synchronously this mating system should shift toward monogamy since there are no additional females with whom to reproduce, particularly in species where males are tied up in mate guarding activities for days or weeks. Increases in host abundance or decreases in predation risk (facilitating roaming among hosts) should make this mating system drift toward pure-search polygyny (see below). Because males defend females, sexual dimorphism in body size and structures potentially usable as weapons should be favored by intrasexual competition. Female mate choice should additionally select for male ornaments. Alternative mating tactics may also be expected here (see Shuster and Wade 2003) (Table 12.1).

Female-centered polygyny as described here has been reported for the anemone-dwelling crab *Inachus phalangium* (Diesel 1986) and the urchin-dwelling shrimp *Athanas kominatoensis* (Nakashima 1987). The hosts inhabited by these crustaceans are intermediate in body size (relative to their symbionts) and occur at moderate abundance in shallow subtidal habitats (Diesel 1986). Unfortunately, information on the intensity of predation off hosts of both symbionts is lacking, but its occurrence should be moderate since these species inhabit subtropical or warm temperate environments where predation pressure should be neither as high as in the tropics nor as low as in cold temperate zones (Diesel 1986, Nakashima 1987). It must be noted that the environment inhabited by *I. phalangium* is also similar to that in which pure-search polygyny is expected. Different populations or individuals in the same population of *I. phalangium* may be experiencing conditions promoting both this mating system and pure-search polygyny at the same time. Comparative studies that explicitly address this possibility would be very interesting. Slight shifts in environmental characteristics could easily cause the individuals to switch from one strategy to another. In general, in these species, chelae are well developed as weapons (see, e.g., Nakashima 1987). In *A. kominatoensis*, small males change sex to females if they have not been successful in copulating with females early during
the reproductive season, while small males of *I. phalangium* may attempt sneaking copulations with females even if these are guarded by large dominant males (Diesel 1986, Nakashima 1987). As predicted, these two species exhibit marked sexual dimorphism and alternative mating tactics.
Pure-Search Polygynandry of Mobile Females

Pure-search polygynandry should evolve when hosts are morphologically complex, large enough to support many symbionts at the same time and highly abundant and when predation risk off hosts is low. Under these circumstances, both males and females should move freely and frequently among and within hosts. Females are expected to be uniformly dispersed among hosts. Host guarding is constrained by the invasion rate and consequent high cost of defense. High host morphological complexity and large size also render their monopolization ineffective. Under these circumstances, males should (p.261) maximize their reproductive success by roaming within and among hosts in search of females. As soon as receptive females are found, males should mate and abandon them immediately to continue searching for other receptive females. On the other hand, females may reject male advances and attempt to choose and mate high-quality males among those visiting them. Multiple mating by females may occur due to female choice or male coercion. Female reproductive concealment (if allowed by female physiology) may evolve as a response to male coercive tactics.

Low breeding synchrony among females should reinforce this mating system while increased breeding synchrony should drive this mating system toward female-centered polygyny, with males guarding females after finding them (see above). Sexual dimorphism in body size should be found in species featuring this mating system. Because males do not invest in defense of females against other males, sexual selection should not favor the development of weapons. Small body size in males should be favored because that leads to an increase in agility and in the encounter rate with potential mating partners and because small body size renders them less conspicuous to predators (see chapter 7).

No studies on the mating system of symbiotic crustaceans inhabiting abundant, large, morphologically complex hosts have been reported, where pure-search polygynandry of mobile females should occur. However, observations on the porcellanid crab *Liopetrolithes mitra* that inhabit an abundant, large, and morphologically complex sea urchin suggest that this species may feature this mating system (Baeza and Thiel 2000, Thiel et al. 2003; Fig. 12.1). This and
other symbiotic crustaceans may perceive abundant, large, and morphologically complex hosts not as individuals but rather as patchy microhabitats.
Pure-Search Polygynandry of Sedentary Females

Pure-search polygynandry of sedentary females should evolve when hosts are extremely small (supporting no more than a single symbiont) and (1) when host abundance is low/moderate and predation risk off hosts is high/moderate, or alternatively, (2) when predation risk is low while host abundance is high/moderate (Fig. 12.4). Under these circumstances, host switching is constrained, but not severely, with both males and females moving among hosts infrequently. Host guarding is favored in males and females. Host monopolization is efficient regardless of their morphological complexity because of small host body size. This combination of factors results in females being uniformly dispersed among hosts at low abundance (i.e., only one female per host) that makes host guarding by males less profitable than roaming in search for females. Therefore, males maximize their reproductive success by infrequently roaming among hosts in search of receptive females. As soon as a female is found, the male should mate and abandon her immediately to continue searching for other receptive females. In turn, females should choose to mate with high-quality males among those visiting them. Sperm limitation may occur under these circumstances, and multiple mating by females may be favored. This mating system may drift toward monogamy with increases in predation pressure or increases in host size. As in the previous mating system, sexual dimorphism in body size should be found in these species, with males being smaller than females.

Species such as the urchin-dwelling brachyuran crab *Zebrida adamsii* (Yanagisawa and Hamaishi 1986) and various species of parasitic pea-crabs (e.g., *Pinnotheres pisum*, [p.262] Haines et al. 1994; *Zaops ostreum*, Christensen and McDermott 1958) have been reported living as solitary individuals in/on small hosts that form relatively dense aggregations in temperate or subtropical temperate environments, where predation risk off hosts is moderate. In agreement with our predictions, studies suggest that males roam among host in search of sedentary females that appear to be mated as soon as they are found. After mating, males do not appear to guard females but leave them immediately to continue searching for others (Christensen and McDermott 1958, Yanagisawa and Hamaishi 1986). Males in all these species are significantly smaller (in body size) than females.
Discussion
Our model predicts different mating systems in symbiotic crustaceans depending on the interaction among host characteristics and predation risk. These mating systems are determined largely by how males compete for females. In this sense, this model is similar to others previously proposed (Jarman 1974, Bradbury and Vehrencamp 1977, Emlen and Oring 1977). On the other hand, this model differs from previous ones in its inclusion of the behavior of females when predicting particular mating systems. Females were assumed to optimize their reproductive success by choosing a male with “good genes” and/or “good resources.” Several recent studies have shown that, in various species, females do not appear to maximize their fitness by choosing a single “high-quality” mate, but rather by being polyandrous (see Zeh and Zeh 2003). Females are assumed to acquire genetic benefits by mating with several males per reproductive event, either by biasing paternity toward males with good genes or by increasing the genetic diversity of their offspring (Andersson 1994, Jennions and Petrie 2000). Whether polyandry has a selective advantage or is simply the result of male coercive tactics is at present a topic of heated debate in behavioral ecology (Zeh and Zeh 2003). The manner in which females maximize their fitness, that is, by mate choice or by preference for polyandry, should be considered more thoroughly in future theoretical and empirical studies of mating systems of symbiotic crustaceans. Another important difference between this model and previous ones is that the risk of predation was explicitly considered as a major determinant of the behavior of these small and vulnerable symbiotic crustaceans. Predation pressure has rarely been considered as a parameter of relevance in previous classical models even though its impact on life history traits in many groups of organisms is widely recognized (see chapters 7, 10). Finally, our model relies on the idea of “economic defensibility of resources” (hosts) to predict the strategy played by individuals to acquire mating partners. This concept is pivotal to most previously proposed models too (Emlen and Oring 1977).
Overall, the limited available empirical studies support the association we predicted among mating system, host characteristics, and risk of predation (Table 12.1). Limited space does not allow discussing a large number of less detailed studies that also support the predictions of our model (see Thiel and Baeza 2001). Nonetheless, we propose that an attempt to falsify this model should be considered the next step in order to improve our understanding of mating systems in symbiotic crustaceans. Here, two (p.263) different approaches are proposed: (1) manipulative experimental and (2) comparative.

The manipulative experimental approach exploits the notion that different mating systems are variations of a single theme, as indicated above. This means that different populations of the same species or different species with a common ancestor should feature different mating systems whenever individuals in each population or species are experiencing dissimilar ecological conditions. Shifts from one to another mating system should depend not only on environmental conditions but also on how flexible a species is in terms of behavior, physiology, and additional anatomical attributes (e.g., presence or absence of weapons in males, sperm receptacles in females). For instance, it should be relatively easy for species such as *I. phalangium* to switch from female-centered polygyny to pure-search polygynandry with slight shifts in host abundance or predation pressure that facilitates roaming among hosts. Because most of the changes that males and females require to attain their new optimal mating strategy are behavioral, this shift should be easily accomplished. Overall, it should be possible to manipulate specific environmental characteristics one at a time (i.e., host abundance, distribution) in the field or in the laboratory and examine whether or not the behavioral strategies of males and females shift according to the predictions of this model. In this respect, some observational studies agree with the assumptions and predictions here raised, although manipulative experiments are lacking. For instance, the shrimp *Alpheus immaculatus* features a monogamous mating system in environments where the risk of predation off hosts is relatively high (Knowlton 1980). In contrast, in its sibling species *A. armatus*, which inhabits environments with a lower risk of predation off hosts, males roam more frequently among host individuals in search of extrapair copulations (see
Knowlton 1980, Knowlton and Keller 1983). In general, decreased risk of predation appears to result in an increase in host-switching behavior and the rate of extrapair copulation by males, and a subsequent shift from monogamy to polygyny, as predicted by this model. Another example is the porcelain crab *Allopetrolisthes spinifrons*, in which both males and females shift more frequently among hosts in the intertidal than in the subtidal zone. The risk of predation appears to be higher and hosts are less abundant in the subtidal than in the intertidal zone (Thiel et al. 2003).

The second, comparative, approach examines whether particular ecological conditions and behavioral traits are related in a group of closely related species. However, because phylogenetic relationships are known to bias the strength of environment–trait correlations, this approach needs to take the phylogenetic relationship among the studied species into consideration (chapter 3). Although various recent studies have elucidated the natural relationships of some groups of symbiotic crustaceans (e.g., Morrison et al. 2004) and have described in detail the mating systems of some others (e.g., Knowlton 1980), the information on a particular group is far from complete to test this model within a comparative framework (for comparative approaches in other groups of arthropods, viz., insects and arachnids, see Choe and Crespi 1997).

An interesting feature of our model is that it focuses on organisms using discrete (i.e., small and discontinuous) refuges (i.e., hosts) as habitat. The fact that these crustaceans depend heavily on their hosts means that these hosts strongly affect the spatial distribution of their associates. In particular, the relative body size of hosts, as well as their abundance and morphological complexity, is proposed to affect the way males (p.264) search for and monopolize females and the mate choice behavior of females (Knowlton 1980). Not only symbiotic crustaceans but also various other groups of marine and terrestrial vertebrates and invertebrates inhabit discrete refuges, and predator avoidance is an important issue during their lifetime. Examples include parasitic helminths, parasitoid insects, litter-associated amphibians, insects, and arachnids in temperate and tropical forests, as well as several other arthropods associated with plants and algae in the terrestrial and marine environment, respectively (see Price 1980, Godfray 1994). The predictions of our model should also apply to them.
In agreement with this model's predictions, monogamy has been reported for symbiotic fish inhabiting refuges with characteristics similar to those of hosts whose crustacean associates feature monogamy (i.e., various clownfish species; Hirose 1995). Also, host-resource polygyny has been described for tree-dwelling lizards where the tree represents a discrete host, large enough to allow the cohabitation of several females but small enough to allow its monopolization by a single dominant male (Manzur and Fuentes 1979). Pure-search polygynandry of mobile females appears to be common in “free-living” shrimps associated with seagrasses and seaweeds (e.g., _Palaeomonetes pugio_, Bauer and Abdalla 2001). These seagrasses and seaweeds constitute habitats with characteristics similar to that of large, abundant, morphologically heterogeneous hosts. At last, pure-search polygynandry also appears to occur in various minute insect parasitoids of animal eggs or plants with a relatively large body size (i.e., various species of fig wasps; Godfray 1994).

Limited space precludes discussing many other examples that support the predictions of this model. Whether or not the predictions of this model apply to groups of organisms other than symbiotic crustaceans that inhabit discrete habitats remains to be explored experimentally.

**Future Directions**

In the model here introduced, various other conditions not necessarily related to the “symbiotic environment” but known to affect animal breeding systems were not included. For instance, female reproductive biology was not addressed here, even though this trait is now recognized as setting the stage for the evolution of male reproductive strategies, because it largely determines the reproductive success of males (Eberhard 1996; see also chapter 9). Similarly, the effects of other important life history traits such as the existence of direct development were not included, even though direct development is recognized as a preadaptation for the evolution of extended parental care (chapters 14, 16) and advanced social behaviors (including eusociality; Duffy 1996; see also chapter 18). In general, by considering the elements above and others in future, more sophisticated versions of the present model, it should be possible to increase the diversity of and accuracy with which the mating systems of symbiotic crustaceans are predicted. Phylogenetic constraints should also be taken into consideration because they may limit the
diversity of mating strategies in a particular group of species (see chapter 11). For instance, the fact that sperm storage structures are absent in caridean shrimps (Knowlton 1980) but present in many crabs (e.g., Diesel 1986) indicates that sperm competition and first or last male precedence may be important influences on the mating systems of crustaceans (see chapter 9).

**Summary**

We propose a conceptual model predicting the mating system of symbiotic crustaceans. It assumes that males and females have different optimal mating strategies that they attempt to attain by defending and moving between hosts, and that host characteristics and predation risk limit the behavioral options of symbiotic individuals. Males are assumed to maximize their reproductive success by mating with as many females as possible and females by choosing a male of high quality among those available. Males and females attempt to maximize their reproductive success mostly by modifying two behavioral traits: host guarding and host switching. Predation risk, host abundance, relative size, and morphological complexity are assumed to affect monopolization of and movement among hosts by symbionts, thereby imposing constraints on their mating strategy. Five mating systems are predicted: (1) monogamy when predation risk off hosts is high and hosts are scarce, morphologically simple, and small in body size; (2) host-defense polygyny when predation risk is high and hosts are relatively scarce, morphologically simple, and intermediate in body size; (3) pure-search polygynandry of mobile females when predation risk is low and hosts are abundant, morphologically complex, and large in body size; (4) pure-search polygynandry of sedentary females when predation risk is moderate to high and hosts are moderately scarce and extremely small in body size; and (5) female-centered polygyny when predation risk is moderate and hosts are neither abundant nor scarce and intermediate in body size. Limited empirical evidence available for symbiotic crustaceans appears largely in agreement with the model's predictions.

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