



Social monogamy in the crab *Planes major*, a facultative symbiont of loggerhead sea turtles



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ABSTRACT

Studying how host characteristics and ecology affect the mating systems of symbiotic crustaceans offers an opportunity to understand how ecological factors contribute to the evolution of different animal mating systems. In theory, symbiotic crustaceans should display social monogamy with long-term heterosexual pairing when hosts are relatively small in body size and structurally simple, and when hosts have relatively low abundance in habitats where the risk of mortality for symbionts (e.g., predation) away from hosts is high. We test this prediction in the mating system of the flotsam crab (*Planes major*) and its facultative association with loggerhead sea turtles (*Caretta caretta*). First, we found that the overall population and sex distributions were non-random and crabs inhabited host turtles as heterosexual pairs more frequently than expected by chance, which supports the hypothesis that *P. major* is socially monogamous on *C. caretta*. Second, we found that male crabs pair with females regardless of their reproductive state, male–female pairs do not display size-assortative pairing, crab body size and host turtle body size are not correlated, and crabs display reverse sexual dimorphism in body size and conventional sexual dimorphism in weaponry. These results do not support the hypothesis that social monogamy in *P. major* is always long term. Instead, our results suggest that the duration of social monogamy in *P. major* is likely variable and may involve some degree of host switching and intra-sexual (mostly male–male) competition. Our results were only partially consistent with theoretical considerations for how host characteristics and ecology affect the mating systems of symbiotic crustaceans, and future studies should focus on quantifying the degree and direction of host switching to better understand the factors that affect the duration of monogamous pairing when *P. major* associates with *C. caretta*.

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1. Introduction

The evolution of different animal mating systems is ultimately determined by specific ecological factors that dictate the spatial and temporal distribution of available resources and mates (Emlen and Oring, 1977). For symbiotic crustaceans that live in or on distinct host species, these

ecological factors are defined in large part by the morphology and ecology of their hosts (Thiel and Baeza, 2001). Baeza and Thiel (2007) outline a general framework for understanding how host characteristics and ecology affect the mating system and social behavior of symbiotic crustaceans. Under this theoretical framework, reproductive strategies of symbiotic crustaceans can be predicted based on four parameters: (1) host relative body size, (2) host structural complexity, (3) host abundance, and (4) the risk of mortality for symbionts away from hosts. These characteristics are considered critical in controlling the frequency of host switching and the capacity for host monopolization, and therefore the adoption of different mating systems (e.g., monogamy, pure polygamy or various forms of polygyny and polyandry). Studying how host characteristics and ecology affect the mating systems of

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symbiotic crustaceans offers an opportunity to understand how ecological factors contribute to the evolution of different animal mating systems.

Among other mating systems, Baeza and Thiel (2007) outline a clear set of conditions for when symbiotic crustaceans should be socially monogamous and form long-lasting heterosexual pairs. Social monogamy should be favored when hosts are relatively small in body size and structurally simple, and when hosts have relatively low abundance in habitats where the risk of mortality for symbionts (e.g., predation) away from hosts is high. These conditions constrain movements among hosts, making host monopolization the favored behavior for both male and female symbionts due to host scarcity and the value that hosts offer as refugia (Baeza and Thiel, 2007). Because spatial constraints allow only a small number of individuals (e.g., two) to cohabitate in or on the same host, both males and females maximize their reproductive behavior by cohabitating with a member of the opposite sex (Baeza, 2008). Under these circumstances, resources (i.e., hosts) and mates tend to be distributed more uniformly across a dangerous environment, which makes it difficult for individuals to monopolize multiple mates or roam among hosts in search of additional mates (Baeza and Thiel, 2007). Thus, symbionts inhabiting small, simple, sparse hosts in habitats where mortality risk is high away from hosts should tend to remain with an individual host and heterosexual partner for extended periods of time and adopt a monogamous mating system (Baeza and Thiel, 2007). Studies on the mating strategies of symbiotic crustaceans that consider the morphology and ecology of their hosts mostly support this hypothesis (Baeza, 2008, 2010; Thiel and Baeza, 2001). However, other studies have found that some symbiotic crustaceans inhabiting small, simple, and sparse hosts are not strictly monogamous and display some degree of male promiscuity (Baeza et al., 2011). Additional empirical studies are needed to test the consistency and generality of these theoretical predictions.

In this study, we test the hypothesis of Baeza and Thiel (2007) that symbiotic crustaceans living in association with small, simple, sparse hosts in habitats where there is a high risk of mortality away from hosts exhibit monogamy and long-lasting heterosexual pairing. We test this hypothesis in the mating system of the flotsam crab (*Planes major*) and its facultative association with loggerhead sea turtles (*Caretta caretta*). *Planes* crabs also live on pelagic flotsam and jetsam, but sea turtles represent higher quality substrata (Dellinger et al., 1997; Frick et al., 2004). Turtle hosts are relatively large in body size compared to their crab symbionts (*C. caretta* = 32–94 cm curved carapace length—this study; *P. major* = 8.3–26.8 mm carapace width—this study). However, *Planes* crabs are almost exclusively found hiding within the supracaudal and inguinal space of host turtles (Fig. 1; Dellinger et al., 1997; Pfaller et al., 2014), making the specific area inhabited by

crabs relatively small and structurally simple. Moreover, although host turtles may concentrate at oceanic convergent zones (Polovina et al., 2000, 2004), they tend to be relatively sparse in the marine environment (0.58–0.75 turtles km⁻²—Seminoff et al., 2014), especially compared to other hosts of symbiotic crustaceans (59,000 and 200,000 hosts km⁻²—extrapolated from Baeza et al., 2011 and Peiró et al., 2012, respectively). Because crabs also show strong reluctance to stray from rafts and limited swimming endurance (Davenport, 1992), mortality risk for crabs off hosts is also assumed to be high. These factors should limit the ability of crabs to switch among turtles in search of additional sexual partners. In theory, the monopolization of such discrete, sparse and valuable resources (i.e., the supracaudal and inguinal space of sea turtles) should favor monogamy with long-term heterosexual pairing (Baeza, 2008; Baeza and Thiel, 2007). In agreement with this prediction, *P. major* is frequently found in male–female pairs on *C. caretta* (Carranza et al., 2003; Frick et al., 2011; Pons et al., 2011), and congeneric *Planes minutus* associated with *C. caretta* in the North Atlantic Ocean are found in male–female pairs more often than expected by chance (Dellinger et al., 1997). However, there is no detailed study that tests the specific hypotheses needed to determine whether *P. major* displays social monogamy on sea turtles or whether heterosexual pairing by *Planes* crabs on sea turtles is long term. Because our understanding of how host traits (i.e., relative body size, morphology, and abundance) influence the reproductive strategies of symbiotic crustaceans comes primarily from studies of symbionts living in or on benthic macro-invertebrates, this study represents a novel test of theory in a host-vertebrate, symbiont-invertebrate system.

If *P. major* is socially monogamous on *C. caretta*, then we expect to find that (1) the population distribution of crabs on turtles is non-random, (2) two crabs/turtle are found more often than expected by chance, and (3) the sex distribution of crabs in pairs is non-random with male–female pairs being found more often than expected by chance. Moreover, if heterosexual pairing is long term, as opposed to one-time or serial monogamy, then we expect to find that (1) males pair with females regardless of their reproductive state (e.g., the presence/absence of eggs and egg developmental stage), (2) male–female pairs display size-assortative pairing, (3) crab body size is positively correlated with host turtle body size, and (4) crabs display little to no sexual dimorphism in body size and weaponry (e.g., chelipeds used for intra-sexual aggression) (Baeza and Thiel, 2007; Thiel and Baeza, 2001). Support for (1) would indicate that males do not abandon females after copulation in order to roam in search of other receptive females (Diesel, 1986, 1988; van der Meeren, 1994). Support for (2) would indicate that pairs have grown under similar space- and resource-related constraints for long periods of time (Adams et al., 1985; Baeza, 1999, 2008). Support for (3) would indicate that crab growth rates are related to or constrained by host turtle growth rates over time such that crabs remain on the same host, presumably with the same partner, for long periods of time (Baeza, 2008). Support for (4) would indicate that selection for larger body size and weaponry in males is relaxed due to the rarity of host switching and male–male competition (Baeza, 2008; Baeza and Thiel, 2007; Shuster and Wade, 2003). Collectively, support for these characteristics would represent a strong indication of a socially monogamous mating system in which heterosexual pairing is long term (Baeza, 2008, 2010; Baeza and Thiel, 2003; Knowlton, 1980). These predictions are frequently tested when evaluating the mating strategies of symbiotic crustaceans (Baeza, 2008; Baeza et al., 2011, 2013; De Bruyn et al., 2009; Peiró et al., 2012).

2. Methods

2.1. Collection of crabs

Individuals of *Planes major* were collected from loggerhead sea turtles (*Caretta caretta*) at four different localities: (1) Japan, along the east coast of Muroto on the island of Shikoku (33.28°N, 134.15°E),



Fig. 1. *Planes major* heterosexual pair hiding within the supracaudal space of a juvenile loggerhead sea turtle, *Caretta caretta* (tail pulled aside to show crabs). Photo courtesy of Ricardo Santos.

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