



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



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ARTICLE INFO

Article history:

Received 9 June 2014

Received in revised form 5 August 2014

Accepted 7 August 2014

Available online xxxx

Keywords:

Mating system evolution

Monogamy

Planes

Sea turtle

Symbiosis

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



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.

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),

(2) Mexico, off Isla Magdalena on the Pacific coast of Baja California Sur (25.1–25.3°N, 112.2–112.5°W), (3) Peru, offshore along the central and southern coast (12–18.3°S, 72–80°W), and (4) Brazil, along the southern coast (27–34°S, 44–51°W) to approximately 1000 km offshore to the Rio Grande Rise (31°S, 34.5°W). In Japan, turtles were incidentally captured by large pound net fisheries between 4 November 2010 and 24 November 2011. In Mexico, turtles were captured by hand from a small fishing boat between 3 July 2011 and 21 October 2011. In Peru, turtles were incidentally captured by artisanal longline fisheries between 10 January 2011 and 20 January 2012. In Brazil, turtles were incidentally captured by longline fisheries between 5 July 2004 and 11 July 2006. All turtles were removed from nets and longlines within 12 hours of initial capture. Once onboard, all turtles (dead or alive) were thoroughly inspected for *P. major* within 5 minutes (especially within the supracaudal and inguinal space of turtles), except in Japan where turtles were inspected within 3 hours. All observed crabs from each turtle were captured by hand and placed immediately in separate containers of 75–95% ethanol, or frozen and subsequently transferred to ethanol. Turtles were also measured for curved carapace length (CCL) using a flexible measuring tape (precision = 0.5 mm).

In the laboratory, all crab specimens were counted, sexed based on external characters (primarily relative abdomen width; wide in females, narrow in males, indistinguishable in juveniles—Hartnoll, 1978, 1982), and measured for carapace width (CW), cheliped length (CL) and cheliped height (CH) to the nearest 0.01 mm using Vernier calipers. Each female crab was identified as either ovigerous or non-ovigerous based on the presence or absence of eggs underneath the abdomen. When present, each egg mass was removed and photographed under a stereomicroscope, and the embryos were classified based on the following characters (Hartnoll, 1963): stage I, embryos with uniformly distributed yolk and no eyespots; stage II, embryos with yolk clustered and visible, but without well-developed eyes; stage III, embryos with well-developed eyes, free abdomens, and thoracic appendages; stage IV, hatching or empty eggs. For each individual host turtle, we had information on host body size (CCL; cm), number of crabs, sex of the crabs (adult male, adult female or juvenile), body and cheliped size of the crabs (CW, CL and CH; mm), egg-carrying state for female crabs (ovigerous or non-ovigerous), and egg stage for ovigerous female crabs (stage I, II, III or IV).

2.2. Testing hypotheses for social monogamy

We tested whether the population distribution of crabs on turtles differed significantly from a random distribution by comparing the observed distribution (number of crabs per turtle) with either a Poisson distribution or a truncated Poisson distribution. We employed a truncated Poisson distribution when the number of turtles harboring zero crabs was unknown (Plackett, 1953). This was the case for Brazil and for all localities pooled. A chi-square test of goodness of fit was used to test for significant differences between the observed and expected (null) distributions (Sokal and Rohlf, 1995). We tested whether 2 crabs/turtle was observed more often than expected by chance alone using a chi-square test of goodness of fit.

For crabs found in pairs on a single host, we tested whether the distribution of male and female crabs differed significantly from a random distribution by comparing the observed distribution of the sexes within pairs (i.e., ♂:♂, ♂:♀, and ♀:♀) with an expected binomial distribution. A chi-square test of goodness of fit was used to test for significant differences between the observed and expected (null) distributions (Sokal and Rohlf, 1995). These statistical procedures were carried out for each sampling locality separately and for all sampling localities pooled.

2.3. Testing hypotheses for long-term pairing

Data from separate sampling localities were pooled for the following statistical procedures. We used chi-square tests of independence to test

whether the presence of eggs or the developmental stage of the embryos carried by females affected the occurrence of males on the same turtle. We used reduced major axis (RMA) regression to test whether male and female crabs found in pairs display size-assortative pairing with respect to body size (CW; mm). We used RMA regressions to test for correlations between turtle body size (CCL; cm) and crab body size (CW; mm) for both male and female crabs.

We used a *t*-test to examine differences in body size (CW; mm) between male and female crabs. In decapod crustaceans, the chelipeds serve as weapons during intra-sexual interactions (Hartnoll, 1978, 1982). We examined whether cheliped size increased linearly with body size in male and female crabs. Using the allometric model $y = ax^b$ (Hartnoll, 1978, 1982), we examined the scaling relationships between carapace width (independent variable) and cheliped length and height (CL and CH, respectively; dependent variables). The slope *b* of the log–log RMA regression represents the rate of exponential increase ($b > 1$) or decrease ($b < 1$) of each measurement relative to body size (CW; mm) of crabs. To determine if the relationships deviated from linearity, *t*-tests were used to test if the estimated slope *b* deviated from the expected slope of unity (Sokal and Rohlf, 1995). If the structures grow more or less than proportionately with a unit increase in body size of crabs, then the slope should be greater or less than unity, respectively (Hartnoll, 1978). Lastly, we used analysis of covariance (ANCOVA) to test for differences between males and females in the slope of these scaling relationships.

3. Results

A total of 178 crabs (78 males, 91 females and 9 juveniles) was collected from 111 loggerhead sea turtles (*Caretta caretta*) captured at the four different localities (Table 1). The number of crabs per turtle varied between 1 and 4 with a mean of 1.60 ± 0.66 (s.d.). A total of 149 turtles was found without crabs (Table 1). Turtle densities, estimated by dividing the number of turtles captured by the total area (km²) encompassed by the widest GPS locations in each locality, ranged from 0.03 turtles km⁻² (Mexico) to 7.9×10^{-4} turtles km⁻² (Brazil).

3.1. Testing hypotheses for social monogamy

The population distribution of *P. major* on *C. caretta* was significantly different from a random distribution in Japan ($X^2_2 = 14.30$, $P = 0.0008$; Fig. 2A) and Mexico ($X^2_3 = 16.03$, $P = 0.018$; Fig. 2B), and not significantly different from a random distribution in Peru ($X^2_4 = 7.48$, $P = 0.11$; Fig. 2C) and Brazil ($X^2_4 = 8.29$, $P = 0.082$; Fig. 2D). For all localities pooled, the population distribution differed significantly from a random distribution (chi-square test of goodness of fit: $X^2_3 = 25.49$, $P = 0.0001$; Fig. 2E). We found turtles hosting two crabs more often than expected by chance in each locality separately (chi-square test of goodness of fit: Japan, $X^2_1 = 6.30$, $P = 0.013$; Mexico, $X^2_1 = 6.72$, $P = 0.0095$; Peru, $X^2_1 = 6.67$, $P = 0.01$; Brazil, $X^2_1 = 4.66$, $P = 0.044$; Fig. 2A–D, respectively) and for all localities pooled (chi-square test of goodness of fit: $X^2_1 = 9.25$, $P = 0.0024$; Fig. 2E).

For crabs found in pairs, heterosexual pairs were found more frequently than expected by chance in each locality separately (chi-square test of goodness of fit: Japan, $X^2_2 = 10.0$, $P = 0.0067$; Mexico, $X^2_2 = 6.53$, $P = 0.038$; Peru, $X^2_2 = 10.0$, $P = 0.0067$; Brazil, $X^2_2 = 15.17$, $P = 0.005$; Fig. 3A–D, respectively) and for all localities pooled (chi-square test of goodness of fit: $X^2_2 = 39.47$, $P < 0.0001$; Fig. 3E). Collectively, these results support the hypothesis that *P. major* displays a socially monogamous mating system on *C. caretta*.

3.2. Testing hypotheses for long-term pairing

Of the 45 females found in heterosexual pairs, 25 (55.5%) were ovigerous (females carrying stage I, II, III and IV = 9, 10, 5 and 1, respectively). Of the 28 solitary females, 13 (46%) were ovigerous (females

Table 1
Population and sex distribution of *Planes major* associated with loggerhead sea turtles, *Caretta caretta*.

Locality	Turtle data		Crab data										
	N ₁	N ₀	N	♀	♂	♂:♀	♀:♀	j:♀	j:j	♀:♀:♀	♂:♀:♀	♂:♂:♀	♂:♀:j
Japan	27	116	37	6	11	10	0	0	0	0	0	0	0
Mexico	25	31	37	7	6	9	1	1	1	0	0	0	0
Peru	18	2	32	4	2	10	0	0	0	1	0	1	0
Brazil ^a	41	–	72	11	6	16	1	2	0	0	2	1	2
Total	111	–	178	28	25	45	2	3	1	1	2	2	2

Notes. N₁, number of turtles with at least one crab; N₀, number of turtles with zero crabs; j, juvenile crab.
^a The number of turtles without crabs in Brazil was not quantified due to logistical limitations.

carrying stage I, II, III and IV = 4, 5, 3 and 1, respectively). The proportion of paired versus solitary females that were ovigerous was not significantly different ($\chi^2 = 0.58$, $df = 1$, $P = 0.44$). The proportion of females carrying eggs at each developmental stage did not differ between solitary and paired females (chi-square test of independence: $\chi^2 = 1.42$, $df = 3$, $P = 0.70$). Thus, males were paired with females randomly with respect to the presence/absence of eggs and egg developmental stage.

We found a weak positive, but non-significant, correlation in body size between males and females forming heterosexual pairs (RMA regression: $r^2 = 0.073$, t-test; $t = 1.84$, $df = 1,43$, $P = 0.073$) (Fig. 4),

indicating a lack of size-assortative pairing. Turtle body size ranged from 32 cm CCL to 93.5 cm CCL (mean = 61 cm CCL), and crab body size ranged from 8.3 mm CW to 26.8 mm CW for females (mean = 17.8 mm CW) and 8.4 mm CW to 23.9 mm CW for males (mean = 16.3 mm CW). We found no correlation between turtle size and female crab size (RMA regression: $r^2 = 0.002$, t-test; $t = 0.44$, $df = 1,84$, $P = 0.66$) and a weak, but positive, statistically significant correlation between turtle size and male crab size (RMA regression: $r^2 = 0.068$, t-test; $t = 2.27$, $df = 1,71$, $P = 0.03$) (Fig. 5).

We found a significant difference in CW between males and females (males < females: t-test; $t = 3.27$, $df = 77$, $P = 0.0016$; Fig. 6A),

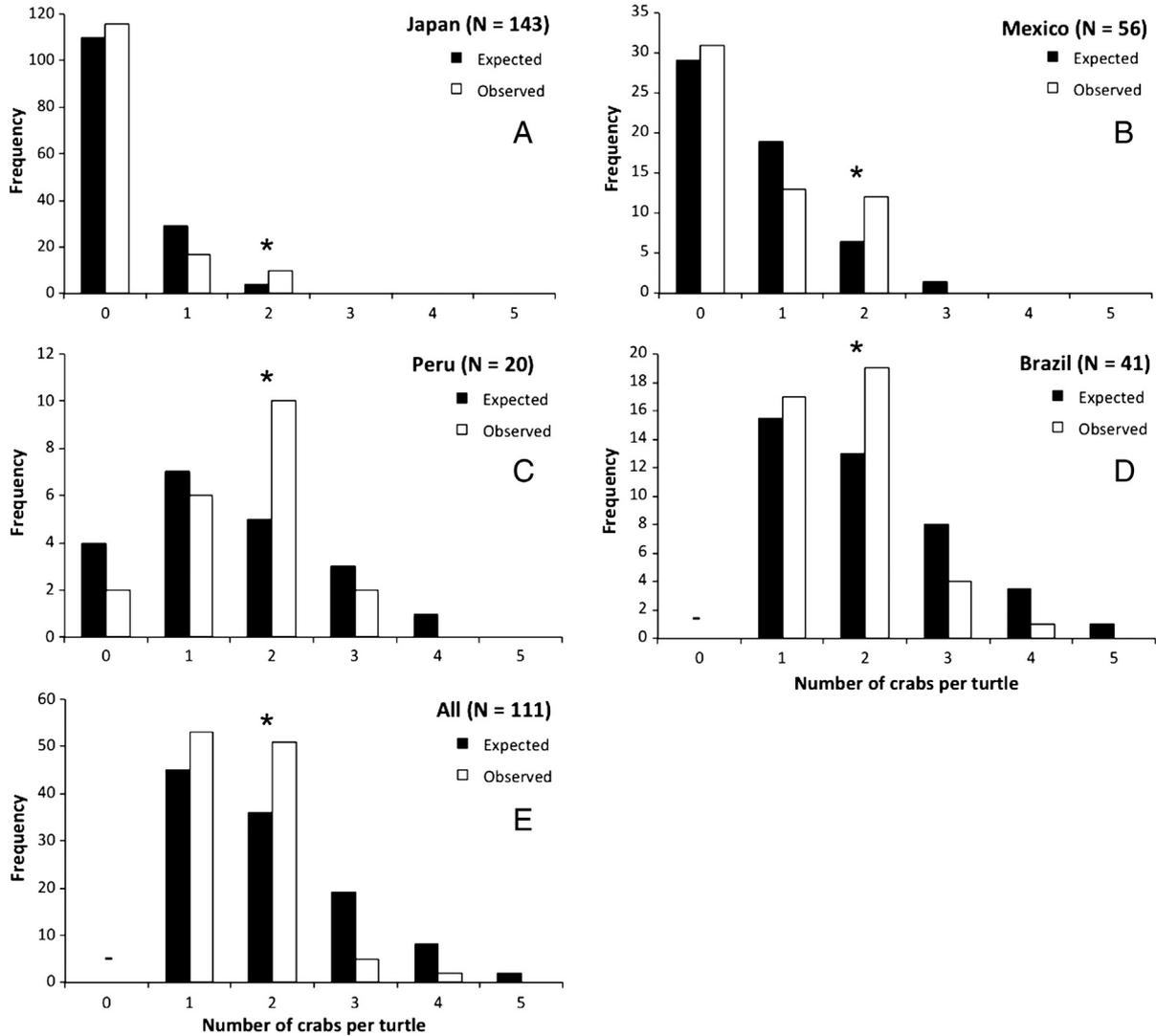


Fig. 2. Population distribution of the crab *Planes major*, symbiotic with the loggerhead sea turtle, *Caretta caretta* in (A) Japan, (B) Mexico, (C) Peru, (D) Brazil, and (E) all four locations pooled. Observed frequency of crabs on turtles differed significantly from the expected random distribution (Poisson or truncated Poisson) for turtles in Japan and Mexico, and for the pooled data. Two crabs were found more often than expected by chance for turtles in each locality separately and for the pooled data. Sample sizes indicate numbers of turtles.

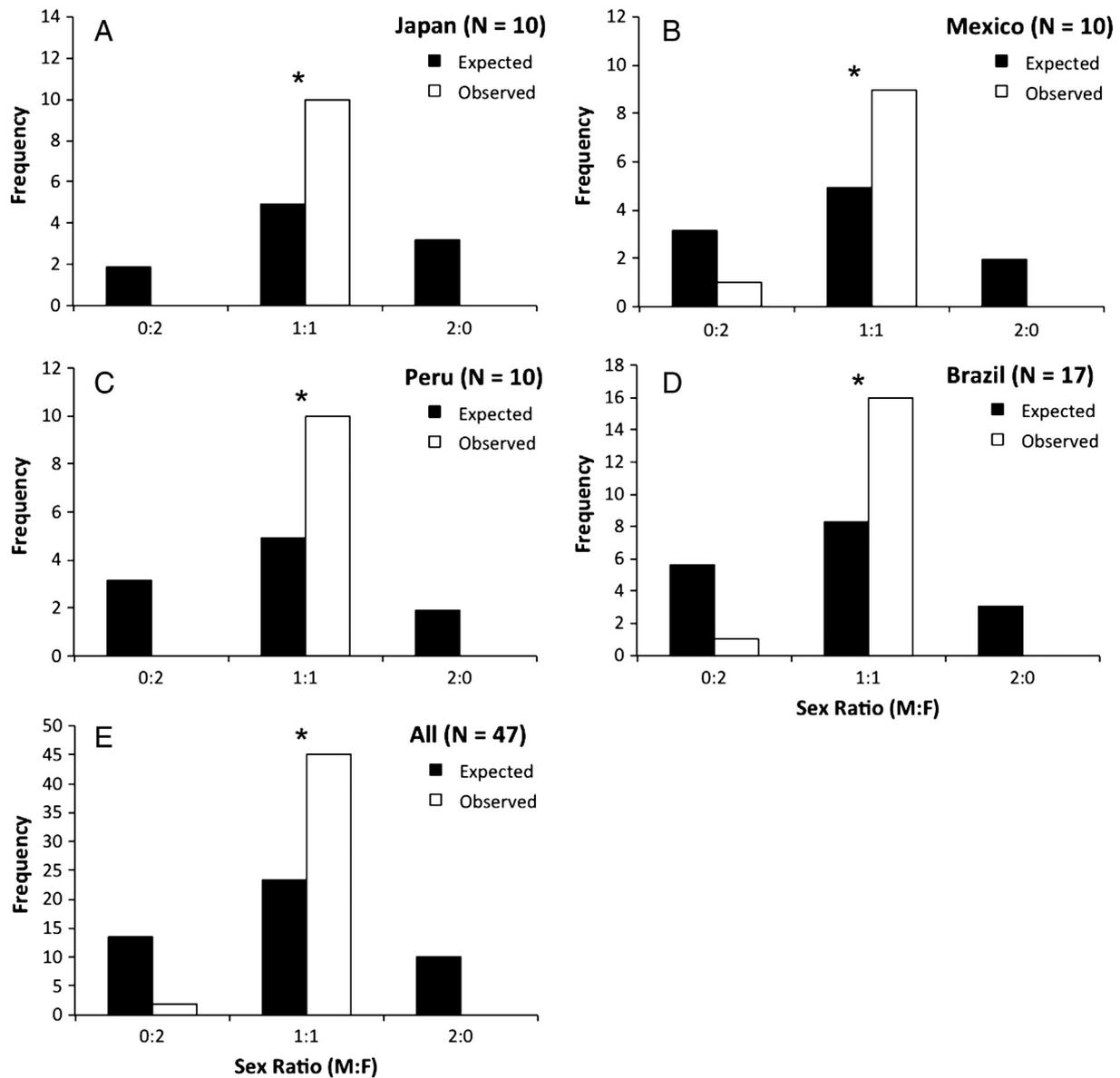


Fig. 3. Male–Female association pattern of *Planes major* found as heterosexual pairs on loggerhead sea turtles, *Caretta caretta* in (A) Japan, (B) Mexico, (C) Peru, (D) Brazil, and (E) all four locations pooled. Observed frequency of heterosexual pairs differed significantly from the expected binomial random distribution. Sample size indicates number of pairs.

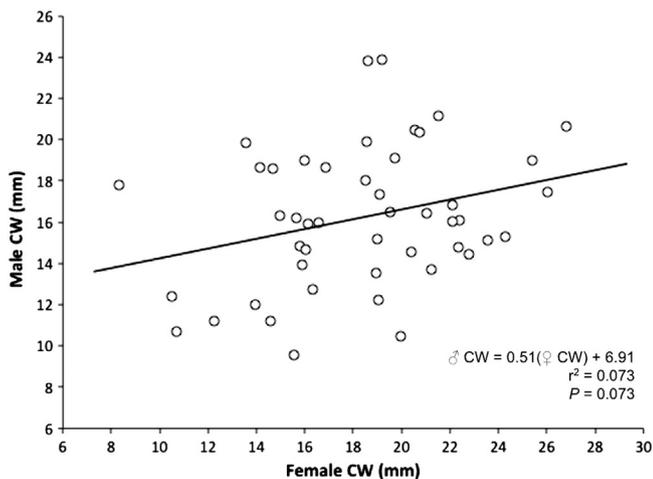


Fig. 4. Relationship between carapace width of females and males of *Planes major* found as heterosexual pairs within the supracaudal/inguinal space of the loggerhead sea turtles, *Caretta caretta*. Data from all four sampling sites were pooled.

indicating reverse sexual dimorphism with respect to body size. In both males and females, the slopes of the relationship between body size and cheliped length and height were significantly greater than 1.0 (positive allometry) (Table 2; Fig. 6B). The growth of cheliped length and height relative to body size was significantly greater in males than in females (ANCOVA: CL, interaction term F-value = 7.05, df = 1, $P = 0.009$; CH, F-value = 4.4, df = 1, $P = 0.037$; Table 2), indicating sexual dimorphism in weaponry.

4. Discussion

4.1. Is *Planes major* socially monogamous on *Caretta caretta*?

We hypothesized that if *P. major* is socially monogamous on *C. caretta*, then we would 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. Our results are consistent with this hypothesis: the overall population and sex distributions were

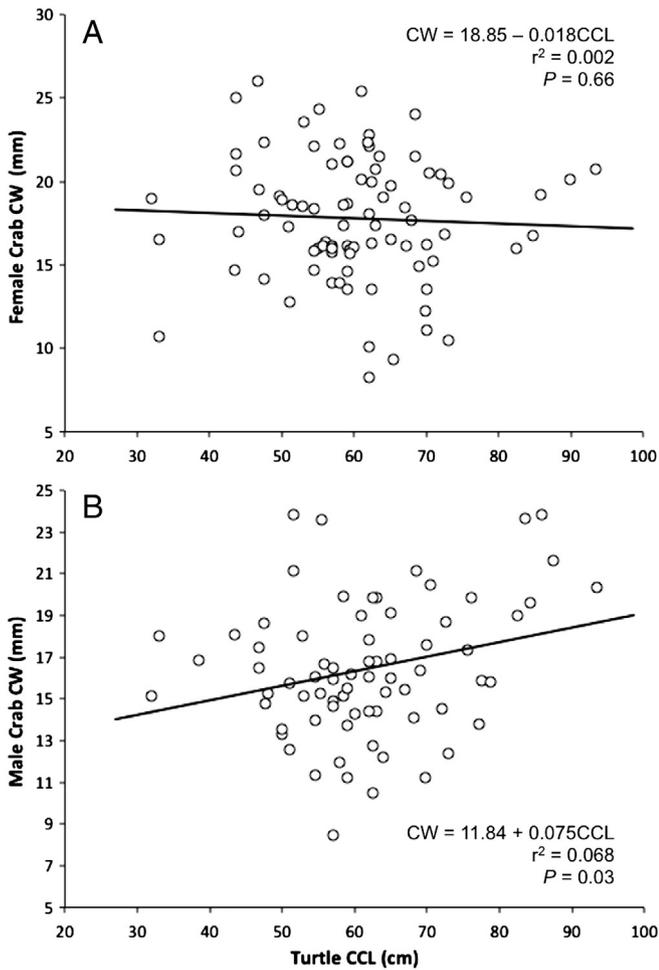


Fig. 5. Relationship between curved carapace length (CCL) of loggerhead sea turtles, *Caretta caretta* and carapace width of (A) females and (B) males of the symbiotic crab *Planes major*. There was a weak positive correlation between host turtle size and male crab size, but not female crab size. Data from all four sampling sites were pooled.

non-random, and crabs inhabited host turtles as heterosexual pairs more frequently than expected by chance. These observations are consistent with theoretical considerations that explain how environmental conditions (e.g., host characteristics and ecology) affect the mating systems of symbiotic crustaceans (Baeza and Thiel, 2007) and with past observations of *P. minutus* on *C. caretta* in the North Atlantic Ocean (Dellinger et al., 1997). Baeza and Thiel (2007) argue that a monogamous mating system should be adaptive under the environmental conditions found when *P. major* lives on *C. caretta*: (1) the supracaudal/inguinal spaces on turtles are defendable resources (functionally small and structurally simple refuges), (2) turtles tend to be sparsely distributed in the marine environment, even in foraging ‘hotspots’ (0.58–0.75 turtles km⁻²—Seminoff et al., 2014), and (3) turtles offer safe refuges in habitats where the mortality risk for crabs away from host turtles is likely high (e.g., from predation, limited swimming endurance, low substrate availability—Davenport, 1992; Hamner, 1995; Shanks, 1983). Under these conditions, host turtles rarely support more than two crabs, and likely because both male and female crabs maximize their reproductive behavior by cohabitating with a member of the opposite sex (Baeza, 2008), we find male–female pairs almost exclusively. These conditions should also constrain movements among hosts, such that once socially monogamous pairs are formed they should tend to remain together on a given host turtle for extended periods of time (see next section).

In agreement with the theoretical predictions outlined by Baeza and Thiel (2007), social monogamy has been reported in numerous other symbiotic crustaceans (e.g., crabs, shrimps and isopods) that inhabit

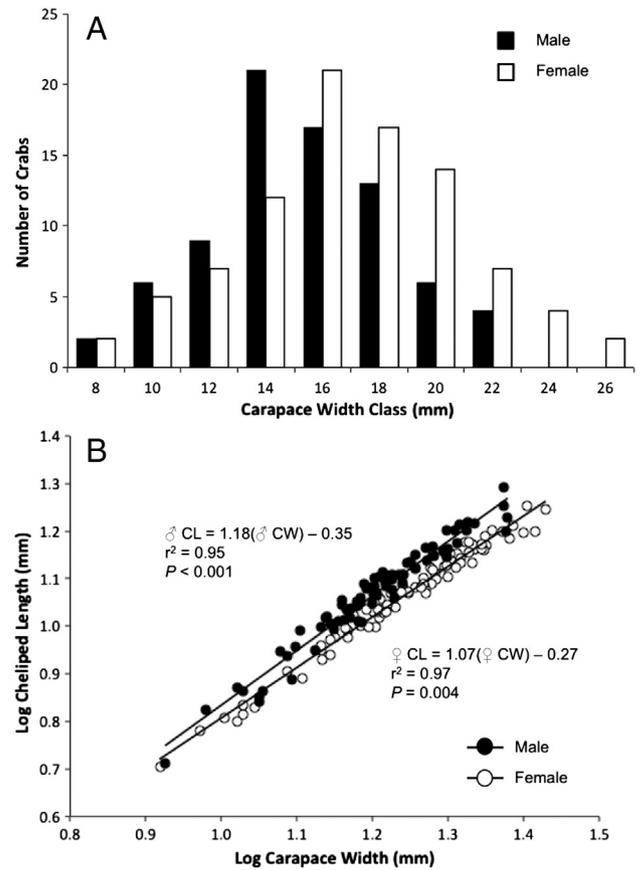


Fig. 6. Patterns of sexual dimorphism in *Planes major*. (A) Size frequency distribution of body size and (B) relative growth of cheliped length as a function of carapace width in males (black bars and circles) and females (white bars and circle).

small, simple, sparse hosts (e.g., cnidarians, echinoderms, bivalves, sponges, and ascidians) in tropical environments where the predation risk for small crustaceans off hosts is presumed to be high (see references in Thiel and Baeza, 2001). Our results also support these predictions, but in a markedly different habitat and type of host. *Planes* crabs are primarily oceanic (occurring in water masses with depths >200 m) and surface dwelling, where their survival, growth and reproduction depend on the availability of floating substrata. Because these valuable resources are generally sparse in the open ocean, symbiosis with sea turtles is likely a highly valuable strategy. Sea turtles may even represent higher quality substrata than inanimate flotsam (Dellinger et al., 1997; Frick et al., 2004). Thus, as in other symbiotic crustaceans, associations with hosts that are both scarce and highly valuable make host guarding or host monopolization an adaptive behavior (Baeza and Thiel, 2007). The subtle difference between this turtle–crab system and other host–symbiont systems is that other sources of mortality (e.g., swimming exhaustion and low host or substrata availability)—in addition to predation—may be important for understanding the mating strategies of symbiotic crustaceans. Therefore, we argue that the theoretical predictions outlined by Baeza and Thiel (2007) can be made more general by considering all sources of mortality away from hosts, not solely predation pressure.

Host scarcity and risk of mortality alone do not necessarily lead to social monogamy. The size and complexity of symbiotic hosts must also constrain the number of symbionts, such that monopolization of a given host is energetically feasible for only a small number of symbionts (e.g., two) (Baeza and Thiel, 2007). Symbiotic crustaceans associated with relatively large and morphologically complex hosts often live in large structured or unstructured groups and display polygynous mating systems (Thiel and Baeza, 2001). Interestingly, *Planes* crabs that

colonize flotsam often live in large, seemingly unstructured aggregations (Dellinger et al., 1997; Frick et al., 2004), while crabs that colonize turtles live either solitarily or in heterosexual pairs. In this facultative system, both turtle and flotsam characteristics (i.e., size, complexity and abundance) might affect the mating behavior of the crabs, such that mating strategies are context dependent and can change depending on the characteristics of the ‘host’ (Baeza and Thiel, 2003). If turtles are just the right size and complexity for two crabs and both males and females benefit by cohabitating with a member of the opposite sex, then symbiosis facilitates social monogamy. More work is needed to test this hypothesis, but it provides a possible mechanism for the origin of obligate symbioses in which symbionts are socially monogamous.

4.2. Is social monogamy in *Planes major* long term?

We hypothesized that if social monogamy in *P. major* is long term, then we would find that (1) males pair with females regardless of their reproductive state, (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. Collectively, the results based on the hypotheses we tested were inconclusive with respect to whether heterosexual pairing is long term. Instead, we suspect that the duration of pairing is variable. This is somewhat inconsistent with the theoretical considerations outlined by Baeza and Thiel (2007). Baeza and Thiel (2007) argue that long-term monogamous pairing should be adaptive under the environmental conditions found when *P. major* lives on *C. caretta* (see above). While we did find some evidence to suggest that heterosexual pairing in *P. major* is somewhat extended, we also found other lines of reasoning to suggest that pairing in *P. major* is not necessarily long term and may involve some degree of host switching and intra-sexual (mostly male–male) competition. Our results also suggest that the line of questioning frequently employed when evaluating the mating strategies of symbiotic crustaceans (Baeza, 2008; Baeza et al., 2011, 2013; Peiró et al., 2012) needs to be expanded to accommodate a greater diversity of symbiotic interactions (e.g., vertebrate–host, crustacean–symbiont symbioses and facultative associations).

Our first hypothesis was that if heterosexual pairing is extended and not one-time or serial monogamy, then we should find that males pair with females regardless of their reproductive state. Our results are consistent with this hypothesis: males cohabitate with females regardless of ovigerous state or stage of developing eggs. In promiscuous and polygamous species, heterosexual pairing is truncated and males are found with receptive females (e.g., carrying no eggs or early-stage eggs) more often than expected by chance alone (*Austinxia aidae*—Peiró et al., 2012). Males in these systems abandon females shortly after copulation and roam in search of other receptive females (Diesel, 1986, 1988; van der Meeren, 1994). Conversely, in monogamous species with extended pairing, males cohabitate with females independent of their reproductive condition (*Pontonia* sp.—Aucoin and Himmelman, 2010; *Pinnixa transversalis*—Baeza, 1999; *Pontonia marginata*—Baeza, 2008). Theoretically, this might be because roaming among hosts in search of other receptive females is too risky (i.e., either physically impossible or too dangerous). This pattern of pairing is consistent with what we found in *P. major* in this study. However, we also found a relatively high percentage of solitary females brooding eggs (46%). Although sperm storage has never been studied in *Planes* crabs, other grapsid crabs do not tend to have extended sperm storage (Rodgers et al., 2011). Thus, if we assume that egg brooding is an indication that female *P. major* in this study had recently cohabitated and mated with a male, then one explanation for the presence of solitary ovigerous females is that males occasionally abandon females after copulation, presumably to colonize different hosts in search of additional mating opportunities. Short-term monogamy with some degree of male promiscuity and roaming has been described in other symbiotic crustaceans (*Pontonia mexicana*—Baeza et al., 2011; *Alpheus armatus*—Knowlton,

1980). Similar roaming behavior by female *P. major* would be undetectable in this study because abandoned males do not show signs of recent cohabitation with the opposite sex (i.e., males are never ovigerous). Based on this line of reasoning, we cannot infer whether or not solitary male *P. major* in this study had recently cohabitated with a female. However, we found similar numbers of solitary male and female crabs (25 and 28, respectively), which suggests that roaming behavior may be similar between the sexes. If males tend to abandon females after pairing temporarily and roam in search of other females, then we might have found more solitary females than solitary males. Nevertheless, our data suggest that pairing in *P. major* is not always long term and may involve some degree of host switching.

Our second hypothesis was that if heterosexual pairing is extended, then we should find that male–female pairs display size-assortative pairing. Our results are not consistent with this hypothesis: body size of male and female crabs found in pairs was not correlated. Size-assortative pairing is expected in species that form long-term monogamous pairs because individuals in pairs would have grown under similar space- and resource-related constraints for long periods of time (Baeza, 2008). Indeed, size-assortative pairing has been reported for various other long-term monogamous free-living and symbiotic crustaceans (Adams et al., 1985; Baeza, 1999, 2008; Mathews, 2002). In the symbiotic and monogamous crustaceans *Pontonia margarita* and *Pinnixa transversalis* male size explains 63.8% and 77.6% of variation in female size, respectively (Baeza, 1999, 2008). In contrast, male body size explains only 7.3% of the variation in female body size in *P. major* (this study) and 0.3% of the variation in female body size in *P. minutus* (Dellinger et al., 1997). This weak correlation suggests that male and female crabs do not cohabitate on the same turtle for long periods of time. Size-assortative pairing is often weak or absent in monogamous species in which pairing is not extended and males (and/or females) switch hosts in search of additional mates (*Pontonia mexicana*—Baeza et al., 2011). Host switching followed by random re-pairing would disrupt any size-assortative pattern, which supports the idea that monogamy is not always long term when *P. major* associates with *C. caretta*.

Our third hypothesis was that if heterosexual pairing is extended, then we should find a positive correlation between crab body size and host turtle body size. Our results are not consistent with this hypothesis: female crab body size and host turtle body size were not correlated, and male crab body size and host turtle body size were only weakly correlated. If male and/or female crabs stay with the same sexual partner and, thus the same individual host for long periods of time, a tight correlation between turtle and crab body size may have been found, as has been reported in various other monogamous symbiotic crustaceans (Adams et al., 1985; Baeza, 1999, 2008). Such strong correlations between host and symbiont body size have been explained in terms of growth limitations experienced by symbiotic individuals that, in turn, are driven by the growth rate of their hosts (Baeza, 2008). Conversely, a weak or non-existent correlation between host and symbiont size (as found in *P. major*) is usually reported for species in which males and/or females switch among hosts rather frequently (*Liopetrolisthes mitra*—Baeza and Thiel, 2000; Thiel et al., 2003). The lack of size-assortative pairing between crabs in male–female pairs (see above) and between crabs and host turtles suggests that *P. major* may have relatively short-term associations with their individual hosts, and consequently, with the other crab inhabiting the same host. Alternatively, the weak correlation between host and symbiont body size in this system could also result from substantial differences in relative growth rate and lifespan between turtles and crabs. Because host turtles grow much more slowly (juvenile *C. caretta* = 10–29% yr⁻¹—estimated from Bjørndal et al., 2003; grapsid crab = 46–64% yr⁻¹—estimated from Flores and Paula, 2002) and live much longer (*C. caretta* = 47–62 yrs.—Dodd, 1988; grapsid crab = 2–4 yr.—Flores and Paula, 2002) than symbiotic crabs, any correlation between host and symbiont size might be unperceivable. Thus, the relationship between host and symbiont

Table 2Relative growth of cheliped size (length and height) in females and males of *Planes major* living on *Caretta caretta*.

Independent variables	N	r ²	Intercept	Slope	Lower limit	Upper limit	Isometric prediction	P-value	Growth type	Sexual dimorphism ^a
Cheliped length										
Females	89	0.97	−0.27	1.07	1.04	1.11	1.0	0.004	P	♀ < ♂
Males	77	0.95	−0.35	1.18	1.12	1.24	1.0	<0.001	P	
Cheliped height										
Females	89	0.93	−0.63	1.14	1.07	1.21	1.0	0.005	P	♀ < ♂
Males	77	0.92	−0.71	1.26	1.18	1.35	1.0	<0.001	P	

Significance level (alpha = 0.05). P-values were corrected using modified t-tests to reflect differences from isometric predictions. Growth type: P = positive allometry.

^a ANCOVA was used to test for differences in slope between males and females. See text for details.

body size may be less informative for understanding the mating system of symbiotic invertebrates living in association with long-lived, vertebrate hosts.

Our fourth hypothesis was that if heterosexual pairing is extended, then we should find that crabs display little to no sexual dimorphism in body size or weaponry. Our results were partially consistent with this hypothesis: males were on average smaller than females, but males have larger chelipeds than females for a given body size. Reverse sexual dimorphism in body size (females > males), as displayed by *P. major*, is found in other monogamous symbiotic crustaceans (*Pontonia* sp.—Aucoin and Himmelman, 2010; *Pontonia margarita*—Baeza, 2008; *Orthotheres tuboe*—Sakai, 1969), while conventional sexual dimorphism in body size (females < males) is common among symbiotic crustaceans that display various polygynous mating systems (Asakura, 2009; Baeza and Thiel, 2007). In theory, reverse sexual dimorphism reflects relaxed selection for larger body size in males because competitive interactions among males are infrequent (Baeza and Thiel, 2007; Emlen and Oring, 1977; Shuster and Wade, 2003). This pattern supports the idea that host switching and male–male competition are infrequent and that heterosexual pairing is somewhat extended in *P. major*. However, *P. major* also displays conventional sexual dimorphism in weaponry. Larger chelipeds in males (relative to females) suggests that males compete for and/or defend receptive females and hosts (turtles and/or flotsam) via overt aggression. Indeed, *P. major* in this study was not found in male–male pairs, but was occasionally found in female–female pairs. If this additional investment in weaponry is an indication of the frequency of agonistic interactions between males, then males likely exhibit some degree of searching and competition for females. In this situation, heterosexual pairing would be necessarily truncated (Baeza and Thiel, 2007). Reverse sexual dimorphism in body size in combination with conventional sexual dimorphism in weaponry are characteristics of other monogamous symbiotic crustaceans in which heterosexual pairing is not long term (*Pontonia mexicana*—Baeza et al., 2011). Interestingly, females also display positive allometry in cheliped size, albeit to a lesser extent than males. This suggests that females also participate in agonistic interactions with other crabs when securing and defending hosts and/or mates, at least temporarily. This is different from other socially monogamous species, in which females allocate relatively fewer resources to weaponry with increasing body size (i.e., negative allometry in cheliped size) (*Pontonia margarita*—Baeza, 2008; *Pontonia mexicana*—Baeza et al., 2011). The observed patterns of the sexual dimorphism and allometry suggest that host switching and competition among crabs are not infrequent, which supports the idea that social monogamy in *P. major* is not necessarily long term.

Collectively, our results suggest that *P. major* does not exclusively exhibit either extended, long-term monogamy or short-term, serial monogamy when associated with *C. caretta*. Instead, our results suggest that the duration of pairing is likely variable. As outlined above, social monogamy in *P. major* was hypothesized to be a function of the size, complexity and abundance of turtle hosts (Baeza and Thiel, 2007). While our data do not support long-term monogamy in *P. major* as predicted by theory (Baeza and Thiel, 2007), these characteristics likely have important consequences for the duration of pairing and the frequency of host switching. Because turtles are highly vagile, the relative

proximity of alternative substrata—other turtles or flotsam—may vary greatly over time and space. Movements among turtles are likely very rare, as turtles tend to be sparsely distributed in the marine environment ($0.03\text{--}7.9 \times 10^{-4}$ turtles km^{-2} —this study), even in foraging ‘hotspots’ ($0.58\text{--}0.75$ turtles km^{-2} —Seminoff et al., 2014). Instead, crabs may colonize or abandon turtles opportunistically when alternative substrata are in close proximity (e.g., when turtles forage along convergent zones that concentrate floating debris—Polovina et al., 2000, 2004). However, crabs likely do not actively abandon turtles when alternatives are unavailable or inaccessible. Under these conditions, the duration of monogamous pairing on host turtles may be highly variable. Nevertheless, the process by which crabs detect turtles, assess the presence or absence of potential mates or competitors, and ultimately decide to colonize or abandon a given host turtle is entirely unknown. Results from our study suggest that crabs may colonize turtles solitarily or cohabitate with members of the opposite sex regardless of body size or reproductive state. However, more work is needed to understand the details of these interactions. Future studies should focus on quantifying the degree and direction of host switching (in the field and in the laboratory) to better understand the factors that affect the duration of monogamous pairing when *P. major* associates with *C. caretta*.

Acknowledgements

We thank all organizations and individuals that either supported or participated in crab collections in Japan (Sea Turtle Association of Japan, H Fukuie, S Watanabe, K Kawano, K Saito, M Hara, S Yamashita, K Hashimoto, K Ebisui and Y Yasuoka), Mexico (David & Lucille Packard Foundation, US Fish & Wildlife Service, ProPeninsula, The Ocean Foundation, Equipo ProCaguama, Grupo Tortuguero, V de la Toba, J Lucero, JM Rodríguez Barón), Peru (Darwin Sustainable Artisanal Fisheries Initiative—Peru), and Brazil (Projeto TAMAR/ICMBio, CEN Consulim). We also thank Jane Brockmann, Gustav Paulay, Martin Thiel and one anonymous reviewer for their helpful comments [SS].

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