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Animal behaviour

Sea turtle symbiosis facilitates social monogamy in oceanic crabs via refuge size

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The capacity for resource monopolization by individuals often dictates the size and composition of animal groups, and ultimately, the adoption of mating strategies. For refuge-dwelling animals, the ability (or inability) of individuals to monopolize refuges should depend on the relative size of the refuge. In theory, groups should be larger and more inclusive when refuges are large, and smaller and more exclusive when refuges are small, regardless of refuge type. We test this prediction by comparing the size and composition of groups of oceanic crabs (*Planes minutus*) living on plastic flotsam and logger-head sea turtles. We found that (i) surface area of refuges (barnacle colonies on flotsam and supracaudal space on turtles) is a better predictor of crab number than total surface area and (ii) flotsam and turtles with similar refuge surface area host a similar number (1–2) and composition (adult male–female pairs) of crabs. These results indicate that group size and composition of refuge-dwelling animals are modulated by refuge size and the capacity for refuge monopolization. Moreover, these results suggest that sea turtle symbiosis facilitates social monogamy in oceanic crabs, providing insights into how symbiosis can promote specific mating strategies.

1. Introduction

Animal populations exhibit different group characteristics depending, in large part, on the capacity for individuals to monopolize available resources (e.g. food, shelter, mates) [1]. When resources are widely available, the per-individual value of monopolizing a resource is low, and resource-defence behaviours become unnecessary [2,3]. In these situations, groups (if present) should be large and inclusive. Conversely, when resources are limited, the per-individual value of monopolizing a resource is high, and individuals should adopt resource-defence behaviours (e.g. territoriality) [2,3]. In these situations, groups should be smaller and more exclusive. Despite clear theoretical expectations, how resource characteristics structure animal groups, and ultimately promote different mating strategies, remains poorly understood.

For animals that require discrete refuges (e.g. burrows, cavities, symbiotic hosts) for protection, mate attraction and/or successful reproduction, the ability (or inability) of individuals to monopolize refuges via competitive exclusion should depend on the size of the refuge relative to the size of the refuge-dwelling animal [3]. Indeed, group characteristics and mating strategies of different species of obligate symbiotic crustaceans that live on or within distinct host species vary depending on the relative size and complexity of their host: large, complex hosts tend to support large, demographically mixed groups of symbionts, whereas small, simple hosts tend to support solitary individuals or heterosexual pairs [4]. Facultative symbioses, in which symbionts also live on non-living hosts that vary

greatly in size, offer us an opportunity to test whether variation in refuge size consistently influences group size and composition within a species. Because refuge size dictates the per-individual value and feasibility of refuge monopolization [3,5], we predict that, regardless of substratum type, groups should be larger and less exclusive when refuges are relatively large and smaller and more exclusive when refuges are relatively small.

We tested this prediction using the oceanic crab (*Planes minutus*), a facultative symbiont of loggerhead sea turtles (*Caretta caretta*). Crabs are commonly found on surface-floating oceanic debris or flotsam, where large, demographically mixed groups seek refuge amongst colonies of stalked barnacles [6,7]. However, crabs that live on sea turtles seek refuge within the supracaudal space of host turtles [6,8], where adult males and females form exclusive pairs, at least temporarily [8]. Positive allometry in weaponry (chelipeds) suggests that crabs physically compete for refuges and/or mates on both substrata [8]. In this system, group size and composition may depend on the total available surface area of living and non-living substrata [6]. Alternatively, if refuge size is a fundamental predictor of group size and composition in this system, then we expect to find that (i) refuge area is a better predictor of crab number than total area on both flotsam and turtles and (ii) flotsam and turtles with similar refuge area host a similar number (i.e. 1–2) and composition (i.e. adult male–female pairs) of crabs. Testing these predictions will inform how resource characteristics structure animal groups and how symbiosis can promote specific mating strategies.

2. Material and methods

(a) Flotsam data

Plastic flotsam was collected along a 2300 km transect through the North Pacific Subtropical Gyre [7]. Once each item was onboard, all crabs were collected and preserved in ethanol (70%). Each item was then characterized by general shape, and total surface area (TSA) was estimated, using standard geometric equations (electronic supplementary material, table S1). Submerged surface area (SSA_F) and ‘refuge’ surface area (RSA_F) were estimated by multiplying TSA by the proportion (estimated visually) of TSA that was submerged underwater while floating and the proportion of TSA that was covered by stalked barnacles (*Lepas* spp.), respectively. In the laboratory, crabs were assigned to species (either *P. minutus* or *Planes marinus*) following Chace [9] and sex and/or stage following Dellinger *et al.* [6], and measured for carapace width (CW; body size proxy).

(b) Sea turtle data

We extracted data on the association between *P. minutus* and 270 oceanic-stage loggerheads from the primary literature: turtle body size (curved carapace length, CCL), sex/stage distribution of crabs and crab body size (CW). To convert linear size measurements of turtles to surface area, we quantified statistical relationships between CCL and (i) turtle submerged surface area (SSA_T; comparable to SSA_F) and (ii) turtle refuge surface area (RSA_T) from a size series of captive and dead loggerheads (electronic supplementary material, figure S1). SSA_T was estimated by modelling the general shape of a turtle body (excluding head and flippers) as one-quarter of an oblong ellipsoid (electronic supplementary material, figure S2). RSA_T was estimated by measuring the linear dimensions of the supracaudal cavity and modelling the space as an isosceles right pentagon with two parallel sides (electronic supplementary material, figure S3).

(c) Genetic analyses

Barcoding fragments of the mitochondrial *cytochrome c oxidase subunit I* gene were sequenced to confirm that (i) *P. marinus* and *P. minutus* are genetically distinct and (ii) *P. minutus* collected in this study (North Pacific) are not genetically distinct from those collected in previous studies (South Pacific and Atlantic). We calculated nucleotide diversity within and pairwise genetic difference between two or three individuals from each species/region.

(d) Statistical analyses

Data were log-transformed (using + 1 correction) to meet statistical model assumptions of normality and homoscedasticity (crab count and size data) and to improve coverage (SSA and RSA). We used the corrected Akaike information criterion to compare the relative fits of crab count data to models with one or both predictors and with different functional forms (to capture potential nonlinear relationships). We compared the relative strength of SSA_F and RSA_F as predictors of crab number by calculating standardized partial regression coefficients in a multiple regression model. We used non-parametric bootstrapping (10 000 random draws with replacement) to compare the sampled distribution of the number of crabs found on turtles versus that of flotsam within the ranges of SSA_T and RSA_T. Lastly, we used linear regressions to test for correlations between mean body size of adult *P. minutus* and SSA_F and RSA_F, and *t*-tests to compare body sizes of adult *P. minutus* from flotsam and turtles.

3. Results

We collected 33 pieces of plastic flotsam, ranging from 16–67 749 cm² TSA, 8–14 905 cm² SSA_F (figure 1a) and 0–2608 cm² RSA_F (figure 1b and electronic supplementary material, table S2). The number of crabs per item ranged from 0 to 130 adult *P. minutus* (figure 1), 0 to 153 *P. minutus* (all stages; electronic supplementary material, figure S4a,b) and 0 to 233 *Planes* (*P. minutus* and *P. marinus*; electronic supplementary material, figure S4c,d and table S2). When only two adult *P. minutus* were present, male–female pairs were found on seven out of nine items. Model comparisons indicated that the best-fit model of crab number was a quadratic function of RSA_F, and standardized partial regression coefficients further verified that RSA_F was a better predictor of crab number than SSA_F (electronic supplementary material, table S3). Qualitatively identical results were found for adult *P. minutus*, all *P. minutus* and all *Planes* (electronic supplementary material, table S3). Mean body size of adult *P. minutus* was not correlated with SSA_F and RSA_F (electronic supplementary material, table S4).

From data on the association between *P. minutus* and loggerhead turtles ($n = 270$; electronic supplementary material, table S5), we calculated averages for SSA_T (4090 cm²; range = 457–8395 cm²), RSA_T (34 cm²; range = 4–66 cm²), number of crabs per turtle (1.63; range = 1–5) and number of adult crabs per turtle (1.51–1.54; range = 1–4). For crabs found in pairs, male–female pairs were found far more frequently than expected by chance ($\chi^2 = 94.1$, $p < 0.001$). Genetic data confirmed that *P. marinus* is distinct from *P. minutus* and that *P. minutus* (synonymous with *P. major*) collected, in this study, are not genetically distinct from those collected in previous studies (electronic supplementary material, table S6).

Within the ranges for SSA_T and RSA_T, the SSA_F and RSA_F of plastic flotsam supported significantly more crabs than did turtles (bootstrapped 95% CI $\neq 0$). However, the difference

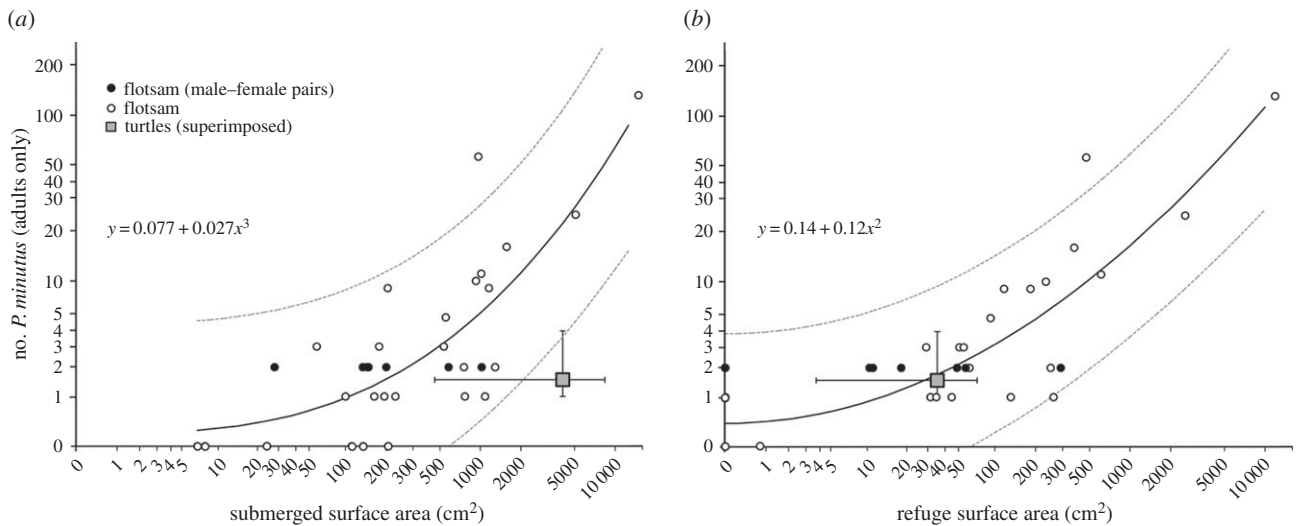


Figure 1. Best-fit models ($\pm 95\%$ CI) of the relationship between (a) submerged surface area and (b) refuge surface area and number of adult *Planes minutus* for flotsam (white and black circles), with mean values for sea turtles superimposed (grey squares; error bars indicate the range of values).

in the number of crabs between flotsam and turtles was significantly different for SSA versus RSA, with much greater values for SSA (mean difference for adult *P. minutus* = -9.04 ; 95% CI = -17.93 , -2.80) than RSA (mean difference for adult *P. minutus* = -0.56 ; 95% CI = -0.99 , -0.11). Qualitatively identical results were found for adult *P. minutus* (figure 1), all *P. minutus* (electronic supplementary material, figure S4a,b), and all *Planes* (electronic supplementary material, figure S4c,d). Collectively, these results show that the refuge surface area provided by plastic flotsam (RSA_F) and turtles (RSA_T) support a similar number and composition of crabs—almost exclusively adult *P. minutus* in male–female pairs.

4. Discussion

We found that refuge area, not total area, is a better predictor of group size and composition of *Planes* crabs living on both plastic flotsam and sea turtles. Refuge size of flotsam varied considerably, and we found a correspondingly wide range in crab number (per plastic item), which increased significantly with refuge area. As refuge area increases, the per-individual cost of monopolizing and defending a refuge space likely outweighs the benefit, allowing groups to become larger and more demographically mixed—many adult *P. minutus* of both sexes, as well as juvenile *P. minutus* and *P. marinus*. However, refuge area provided by smaller colonies of barnacles and turtle hosts of all sizes ($RSA < 80 \text{ cm}^2$; figure 1b) are sufficiently small to make refuge monopolization energetically beneficial to smaller, more exclusive groups of crabs. In these situations, adult male–female pairs of *P. minutus* apparently exclude unwanted conspecific intruders (other adult and juvenile *P. minutus*) and interspecific competitors (*P. marinus*), likely via territorial aggression [8]. Such interaction, however, do not lead to discernible differences in body size among adult *P. minutus* with respect to RSA. Collectively, these results support the prediction that group size and composition of refuge-dwelling animals are modulated by refuge size and the per-individual value and feasibility of refuge monopolization [2–5].

Group size and composition affect fundamental aspects of an animal's biology, including its mating strategy [1]. In the open ocean, where both flotsam and turtles are sparsely distributed, switching 'hosts' in search of additional mating

opportunities is likely dangerous and therefore entails a significant cost [3,4]. Because large colonies of stalked barnacles support many adult crabs (specifically *P. minutus*), individuals can seek additional mating opportunities without leaving the refuge area, which likely promotes a mating strategy that is less exclusive (e.g. polygamy or polygyny). In these situations, the benefits of promiscuity without the risk of 'host' switching likely outweigh the costs of territorial confrontations [6,8]. Conversely, when refuges are small (e.g. small colonies of stalked barnacles or the supracaudal space of sea turtles), the benefits of greater promiscuity (especially for males) cease to outweigh the costs of 'host' switching and refuge monopolization. Such conditions likely promote resource-defence behaviours and make social monogamy advantageous both energetically and reproductively [3,4,8]. Because sea turtles provide refuges within the size range that can be monopolized by two crabs (figure 1b), sea turtle symbiosis specifically promotes social monogamy in *P. minutus* via energetic constraints imposed by refuge size. These results provide a mechanism for how symbiosis can facilitate the adoption of specific mating strategies [4].

Ethics. All data were collected within the ethical standards followed by the Plastics @ SEA North Pacific Expedition (operated by Sea Education Association, Woods Hole, MA). There is no need for research clearance or ethical approval for the collection of crab specimens outside Economic Exclusive Zones.

Data accessibility. Datasets supporting this article have been uploaded as part of the electronic supplementary material. Data from the Plastics at SEA 2012 Expedition are available on the Marine Geoscience Data System (http://www.marine-geo.org/tools/search/entry.php?id=Pacific_Law).

Authors' contributions. J.P. conceived and designed study; M.G. collected field data; J.P. and M.G. performed statistical analyses and composed all sections of the article together. J.P. and M.G. gave final approval for publication and agreed to be accountable for all aspects of the work.

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