

Avoiding disease vs avoiding predation: testing the trade-off in *Panulirus argus*

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ABSTRACT.— Caribbean spiny lobsters, *Panulirus argus* (Latreille, 1804), usually avoid sheltering with conspecifics exhibiting the PaV1 viral disease, yet commonly cohabit with them in large, low-lying artificial shelters called “casitas” that are deployed in shelter-poor habitats in certain fisheries. We tested two hypotheses proposed to explain this finding: (A) that in shelter-poor habitats, healthy lobsters make a trade-off between avoiding disease and avoiding predation; and (B) that the large size of casitas allows segregation between healthy and diseased lobsters. We conducted eight experiments in seawater tanks fitted with two casitas, one empty and one harboring either a healthy or a diseased tethered lobster (“resident”), or both harboring a healthy or a diseased resident. We then introduced six healthy, free-ranging lobsters (FR-lobsters) into each tank (three replicates per experiment) and recorded their location after approximately 40 hrs. Experiments were conducted with and without a predatory triggerfish. Without predators, FR-lobsters used empty casitas and those harboring healthy residents, but avoided casitas harboring diseased residents, preferring to remain in the open. With a predator present, FR-lobsters used empty casitas and those harboring healthy but also diseased residents, suggesting that disease avoidance depends to some degree on availability of alternate shelter and immediacy of predation risk. In larger casitas deployed in a reef lagoon, co-occurrence of wild diseased and healthy lobsters was relatively high, but the probability of finding diseased lobsters segregated from healthy lobsters decreased with increasing number of lobsters. Overall, the results support both hypotheses, reflecting the complex but flexible behavior of *P. argus* under different ecological contexts.

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Caribbean spiny lobsters, *Panulirus argus* (Latreille, 1804), constitute one of the most important fishing resources in the Wider Caribbean Region (FAO 2016). These spiny lobsters are gregarious and tend to share crevice-type shelters in shallow coastal areas and coral reefs (Childress and Herrnkind 1996). The gregariousness of *P. argus*, which is mediated by conspecific chemical attractants (Ratchford and Eggleston 1998) released in the urine (Shabani et al. 2009), underlies the success of two of the most widely used fishing gear to catch these lobsters. In Florida, USA, fishers use sublegal lobsters in traps as live decoys to attract more lobsters into the traps (Behringer et al. 2012), whereas in Cuba, The Bahamas, and certain parts of Mexico, fishers deploy large, low-lying artificial shelters called “casitas,” which consist of a flat slab supported by a frame a few centimeters above the substrate that creates a large, artificial, crevice-providing shelter for multiple lobsters. In Mexico, casitas used in the lobster fishery have a surface area of 1.5–2 m² and have two entrances with a height of 12–15 cm (Briones-Fourzán et al. 2000).

For mobile animals, aggregating with conspecifics may provide benefits, such as cooperative vigilance, group defense, or increased foraging or reproductive opportunities (Lima and Dill 1990). Den-sharing spiny lobsters express group defense behavior, in which lobsters stay in close contact with each other and use their long and spiny antennae in concert to fend off enemies attempting to enter the den (Herrnkind et al. 2001). However, spiny lobsters can also aggressively preclude other lobsters from entering a den, in particular when shelter is scarce or suboptimal (Berrill 1975, Cobb 1981). Thus, in shelter-poor habitats, properly scaled casitas were found to reduce competition for suboptimal natural shelter among juvenile *P. argus*, providing the opportunity for gregariousness and for small juveniles to cohabit with larger conspecifics, which have greater individual and collective defensive abilities (Eggleston and Lipcius 1992, Briones-Fourzán et al. 2007). Aggregating with conspecifics may also have costs, such as increased aggression, and increased transmission of parasites and infectious diseases (Hart 1990, Ward and Webster 2016). Therefore, many social animals, including humans, have developed behavioral strategies (the “behavioral immune system”) that reduce the spread of parasites and pathogens (Loehle 1995, Kiesecker et al. 1999, Curtis et al. 2011, de Roode and Lefèvre 2012).

Wild populations of *P. argus* are affected by *Panulirus argus* Virus 1, or PaV1, an unenveloped DNA virus that develops within the nuclei of host cells. PaV1 first attacks fixed phagocytes in the hepatopancreas, followed by cells in the connective tissue and certain types of hemocytes, but after a few weeks, the infection can become systemic. Severely infected lobsters become lethargic and die, probably from metabolic waste (Shields and Behringer 2004, Shields 2011). Lobsters clinically infected with PaV1 (i.e., diseased) exhibit milky hemolymph that does not clot and a reddish discoloration over the exoskeleton (Shields and Behringer 2004, Lozano-Álvarez et al. 2008). In experimental infections, these signs do not appear until several weeks after inoculation (Behringer et al. 2006). Juvenile lobsters (<50 mm carapace length, CL) are more susceptible to PaV1 than sub-adult (50 to 75–80 mm CL) or adult lobsters (>75–80 mm CL), which can become infected but rarely develop the disease (Behringer et al. 2012, Candia-Zulbarán et al. 2012, Huchin-Mian et al. 2013).

In Florida Bay, Behringer et al. (2006) observed a low level of cohabitation between healthy and diseased lobsters, and in laboratory experiments, they found that healthy lobsters avoided dens containing diseased conspecifics and preferred to share dens with other healthy lobsters. The authors concluded that disease avoidance behavior,

which was later found to be mediated by chemical deterrents released in the urine (Anderson and Behringer 2013, Candia-Zulbarán et al. 2015), could be important in maintaining relatively low prevalence levels.

The discovery that PaV1 could be transmitted by contact (Butler et al. 2008) raised concern about the potential effects of using casitas to harvest *P. argus* (Behringer et al. 2012). Lozano-Álvarez et al. (2008) reported an increase in prevalence of PaV1 in the Puerto Morelos reef lagoon in Mexico between 2001 (the year when PaV1 was first observed in that location) and 2006, but with no effects on lobster density despite relatively high levels of cohabitation between healthy and diseased lobsters in the experimental casitas previously used by Briones-Fourzán et al. (2007). Lozano-Álvarez et al. (2008) proposed two alternative, non-mutually exclusive hypotheses to explain these apparently counterintuitive results: (A) that in shelter-poor habitats (where casitas are usually deployed), healthy lobsters that find a casita occupied by a diseased conspecific make a trade-off between avoiding disease and avoiding predation; and (B) that the shelter area offered by casitas was sufficiently large to allow for segregation of healthy and diseased lobsters in its interior. An important consideration about hypothesis A is that it hinges on the interaction between availability of alternate shelters and level of local predation risk: if the former is low and the latter is high, lobsters may prefer to cohabit with diseased conspecifics than increase their time of exposure to predators by seeking another shelter (Lozano-Álvarez et al. 2008).

In Bahía de la Ascensión, Mexico, where the local lobster fishery is based on the extensive use of commercial casitas, the presence of diseased individuals in casitas did not affect the distribution and aggregation patterns of lobsters in any of three different bay zones (Briones-Fourzán et al. 2012). Moreover, in one of these zones where availability of shelter other than casitas was virtually non-existent, lobsters were actually more crowded in casitas where diseased conspecifics were present, yet this zone had the lowest prevalence of PaV1 in the bay, both clinical (Briones-Fourzán et al. 2012, Candia-Zulbarán et al. 2012) and subclinical [i.e., detected by polymerase chain reaction (PCR), Huchin-Mian et al. 2013]. These results suggest that disease avoidance does not necessarily pay off for healthy lobsters in certain ecological contexts, as suggested by Lozano-Álvarez et al. (2008).

In the Florida Keys, where sponges constitute the main shelter for juvenile *P. argus*, Butler et al. (2015) conducted a field experiment after a massive die-out of sponges resulted in overcrowding of the remaining shelters (small coral heads, crevices) by juvenile lobsters. One day after introducing either a disease or a healthy lobster into crowded shelters, they found that lobster aggregations tended to decrease overall, but significantly more when a diseased conspecific was added than when a healthy conspecific was added. Butler et al. (2015) interpreted this result as evidence that lobsters would rather risk predation and seek another shelter than cohabit with a diseased conspecific. This is an interesting result given that avoiding predation is clearly of overriding importance in determining the fitness of individuals (Lima and Dill 1990), but the issue as related to the use of casitas remains unresolved.

Here, we used experimental and field data to test the two hypotheses proposed by Lozano-Álvarez et al. (2008). The trade-off hypothesis was tested in a suite of laboratory experiments that varied in the presence/absence of alternate shelter, diseased lobsters, and predation risk. We used casitas as shelters in these experiments, although these were much smaller than the commercial casitas due to constraints

imposed by the dimensions of the experimental tanks. Also, instead of testing the response of a single focal lobster, we used groups of lobsters, given that casitas typically harbor multiple lobsters. We expected lobsters to avoid sharing shelters with diseased conspecifics in the absence of predators, but not necessarily in their presence, especially if alternate shelter was unavailable. The shelter area hypothesis was examined by analyzing the level of cohabitation between healthy and diseased lobsters in the experimental casitas deployed on the Puerto Morelos reef lagoon, and testing the effect of the number of lobsters in a casita on the probability of finding diseased lobsters segregated from healthy conspecifics. In general, we expected diseased lobsters to be segregated unless the casita was too crowded.

MATERIALS AND METHODS

LABORATORY EXPERIMENTS

The experiments were conducted in the Unidad Académica de Sistemas Arrecifales, Universidad Nacional Autónoma de México, located at Puerto Morelos, Mexico (20°52'N, 86°52'W). Using scuba diving, we collected juvenile lobsters (38–57 mm CL) by hand in the Puerto Morelos reef lagoon and immediately transferred them to the laboratory. Lobsters were considered as “diseased” if they exhibited milky-white hemolymph (visible through the translucent membrane between the cephalothorax and abdomen) and a reddish discoloration over the exoskeleton (Huchin-Mian et al. 2013), and as “healthy” if they had no clinical signs of disease at all. The presence of PaV1 was not confirmed via PCR assays because (A) the milky hemolymph is diagnostic for PaV1 in *P. argus* (Huchin-Mian et al. 2013); (B) according to Cruz-Quintana et al. (2011), lobsters with a combination of milky hemolymph and reddish discoloration exhibit histopathological damage consistent with a moderate to heavy grade of infection, i.e., grades 2 and 3 in Li et al.'s (2008) severity scale of 0 (no infection) to 3 (heavily infected); and (C) even though lobsters with no macroscopic signs of PaV1 infection might be subclinically infected (i.e., infected but not diseased), conspecific chemical attraction has been shown to be similar toward subclinically infected and uninfected lobsters (Candia-Zulbarán et al. 2015).

Lobsters were segregated by health status in large outdoor tanks kept under shade and provided with multiple shelters (hollow bricks). A continuous seawater flow maintained ambient temperature in the tanks. Lobsters were acclimatized for a maximum of 5 d to avoid potential changes in social behavior due to captivity (Lozano-Álvarez 1996). During acclimatization, lobsters were fed ad libitum with frozen mussels (previously thawed), but were not fed during the experiments (see below).

For experiments that included a predator, we used the queen triggerfish, *Balistes vetula* Linnaeus, 1758, an important predator of juvenile and adult *P. argus* in the Puerto Morelos reef lagoon (Lozano-Álvarez and Spanier 1997, Weiss et al. 2008). Triggerfish (28–45 cm total length) were collected with hand nets in the Puerto Morelos reef lagoon and coral reef. The fish were held in a separate tank and were fed ad libitum with a seafood mixture (shrimp, mussels, squid, and octopus), but were not fed during the experiments.

Experimental Design.—All experiments were conducted in six circular tanks 3 m in diameter and 1 m in height, with a water level of 80 cm. Two casitas were deployed

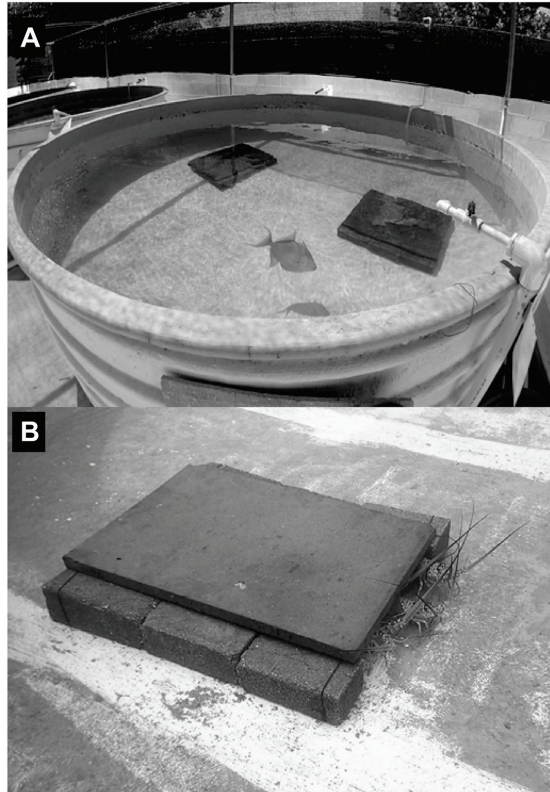


Figure 1. (A) An experimental tank (3 m in diameter, 1 m in height) showing the approximate location of the two casitas as well as a predatory triggerfish (*Balistes vetula*) used in some experiments. (B) A close-up of an experimental casita in a tank with a few sheltered lobsters (*Panulirus argus*). The stone slab measured 60 cm in length \times 40 cm in width, but the bricks supporting the two longer sides of the slab reduced the width to 30 cm. The inner height of the casita was 6 cm.

in each tank, separated from each other by at least 1 m and from the wall of the tank by approximately 50 cm (Fig. 1A). Each casita was constructed with a flat slab 60 cm long \times 40 cm wide supported by two lines of blocks 6 cm in height, thus leaving two entrances 30 cm wide \times 6 cm in height on opposite sides (Fig. 1B).

We conducted eight experiments, which differed in the presence/absence of alternate shelter, diseased conspecifics, and predators (Table 1). In all experiments, one “resident” lobster (either healthy or diseased) was tethered to one of the entrances of either one or both casitas in each tank (Table 1). A loop of nylon thread was tied around the carapace of the resident lobster (between the third and four pereopods). One end of the thread was secured with a swivel clip to the tie while the other end was tied to the block at one of the entrances to the casita. The length of the tether was 20 cm so that the lobster could move between the outside and one-third the length of the inside of the casita. In experiment 1 (E1), one casita harbored a healthy resident, whereas the other was empty. The selection of the casita for the resident lobster was random. In experiment 2 (E2), one casita had a diseased resident and the other was empty. In experiments 3 and 4, both casitas in the tank had one resident lobster each, either healthy (E3) or diseased (E4). The remaining experiments (E5 to E8) were the same as E1 to E4, respectively, but with the addition of a predatory triggerfish (Table

Table 1. Experimental design to test the effect of the absence vs presence of diseased resident (tethered) lobsters, alternate shelter (empty casita), and predation risk on the shelter choice of healthy, free-ranging *Panulirus argus* juvenile lobsters. The experimental unit was a tank 3 m in diameter with two casitas. One casita (X) had either a healthy or a diseased resident lobster, whereas the other casita (Y) was either empty or had also a resident lobster of the same health status as the other casita. In experiments E1–E4 there was no predator, whereas in E5–E8 there was a predatory triggerfish (*Balistes vetula*) per tank. Each experiment had three replicate tanks with six free-ranging lobsters each. The last column gives the *P*-value of a test of heterogeneity in data due to replicate tank (Fisher-Freeman-Halton tests). In all but one experiment (E2), the test was rejected.

Experiment	Casita X	Casita Y	Predator	<i>P</i>
E1	Healthy resident	Empty	Absent	1.000
E2	Diseased resident	Empty	Absent	0.015
E3	Healthy resident	Healthy resident	Absent	0.350
E4	Diseased resident	Diseased resident	Absent	1.000
E5	Healthy resident	Empty	Present	1.000
E6	Diseased resident	Empty	Present	1.000
E7	Healthy resident	Healthy resident	Present	0.196
E8	Diseased resident	Diseased resident	Present	0.085

1). In trials in which only one casita harbored a resident lobster, this casita was called “casita X” and the empty casita “casita Y”. In trials in which both casitas harbored a resident lobster, the casita that was chosen by most free-ranging lobsters at the end of the trial was called casita X and the other was called casita Y.

Once the resident lobsters were in place according to a particular experiment, six free-ranging, healthy lobsters were introduced within a mesh cylinder into the tank at approximately 14:00–15:00 hrs. After an acclimatization period of 1 hr, the mesh cylinder was removed and the lobsters were free to roam the tank. In experiments E5–E8, the triggerfish was introduced into another mesh cylinder at the same time as the lobsters but remained in it for 2 hrs, i.e., 1 hr longer than the lobsters, to allow the lobsters to seek shelter before releasing the fish. On the morning of the second day (after approximately 40 hrs), we recorded the location of each lobster (casita X, casita Y, or exposed). We then extracted all lobsters (and the triggerfish when used) from the tanks. The tanks were then drained and brushed, and the casitas were washed and left to dry until the next trial. There were three replicate tanks (i.e., $n = 18$ free-ranging lobsters) per experiment. Because we only had six tanks, and to avoid potentially confounding effects of season, we interspersed replicates from different experiments across the experimental period (October 2014–September 2015). All lobsters and triggerfish were used only once. The triggerfish were returned to the sea, but the lobsters were not returned to avoid reintroducing sources of infection.

Statistical Analyses.—For each experiment, we first tested for heterogeneity of the data on shelter choice by lobsters (three options: casita X, casita Y, or in the open) due to replicate tank with a 3×3 contingency table using the Freeman-Halton extension of the Fisher exact test (Freeman and Halton 1951), available at Soper (2017a). In all but one experiment (E2), the heterogeneity of data due to replicate tank was rejected (Table 1). With this caveat, we pooled the data of the three replicate tanks of each experiment to compare the shelter choice by free-ranging lobsters between pairs of experiments differing in one of three factors: (1) absence vs presence of diseased resident lobsters, i.e., E1 vs E2, E3 vs E4, E5 vs E6, and E7 vs E8; (2) absence vs

presence of alternate shelter (empty casita), i.e., E1 vs E3, E2 vs E4, E5 vs E7, and E6 vs E8; and (3) absence vs presence of a predator, i.e., E1 vs E5, E2 vs E6, E3 vs E7, E4 vs E8. All comparisons were done with Fisher exact tests on 2×3 contingency table using the Freeman-Halton extension, available at Soper (2017b). In all cases, results were considered significant if $P < 0.05$. Results from each experiment are graphically expressed as percentage of lobsters that chose casita X, casita Y, or remained out (exposed) with 95% confidence intervals. We used the score method with continuity correction (Newcombe 1998) to compute 95% CI for percentages.

REEF LAGOON CASITAS

The field study was conducted in the shallow Puerto Morelos reef lagoon (<5 m in depth), which extends from the coastline to a coral reef tract located 500–2000 m from the coast. The bottom of the lagoon is mostly sand stabilized by extensive mixed seagrass/macroalgal meadows, which constitute adequate settlement habitat for *P. argus* postlarvae and nursery habitat for small juveniles; however, crevice-type shelter for larger juveniles is scarce, causing a population bottleneck (Briones-Fourzán and Lozano-Álvarez 2001). Experimental casitas deployed between 1998 and 2003 on five 1-ha sites significantly increased juvenile lobster density and biomass relative to control sites (Briones-Fourzán et al. 2007). In 2009, 50 casitas (10 per site) were again deployed on the same five 1-ha sites as before, to examine their potential influence on PaV1-disease prevalence (RI Candia-Zulbarán, unpubl data). Each casita was built with a flat cement slab (Durock®) 1.4 m² in surface area, bolted to a double-stack frame made with 3.8 cm inner diameter PVC pipes, leaving an inner shelter area of 1.2 m² and an entrance height of 4 cm. The casitas were surveyed approximately every 3–4 mo. In each survey, we recorded the number of lobsters beneath each casita, their health status (diseased vs healthy), and size. We also recorded the presence of animals other than spiny lobsters in casitas, including potential predators and competitors (e.g., Mintz et al. 1994, Lozano-Álvarez et al. 2007, Briones-Fourzán et al. 2012), as these may produce chemical “noise” potentially masking the scents of diseased lobsters (Atema 2012). Between January 2013 and May 2015, in those casitas that were co-occupied by healthy and diseased lobsters, we further recorded whether the diseased lobsters were “together” with (i.e., grouped) or “segregated” from (i.e., at a distance of more than one body length) the healthy lobsters. If more than one diseased lobster occurred in a casita, we scored “together” if at least one of these lobsters was grouped with healthy conspecifics. Because of the binary nature of the response variable, we used a logistic regression analysis (Warton and Hui 2011) to test the effect of the number of lobsters in a casita (with four levels: 2 lobsters, 3–6 lobsters, 7–10 lobsters, and more than 10 lobsters) on the probability of finding diseased lobsters segregated from healthy lobsters.

RESULTS

LABORATORY EXPERIMENTS

Experiments with no Predators (E1–E4).—In the absence of a predator, with one casita harboring a healthy resident and the other casita empty (E1), free-ranging lobsters used both casitas (40% and 60%) and none remained in the open (Fig. 2A), but when one casita harbored a diseased resident and the other casita was empty (E2), almost 80% of the free-ranging lobsters used the empty casita, with 10% remaining in

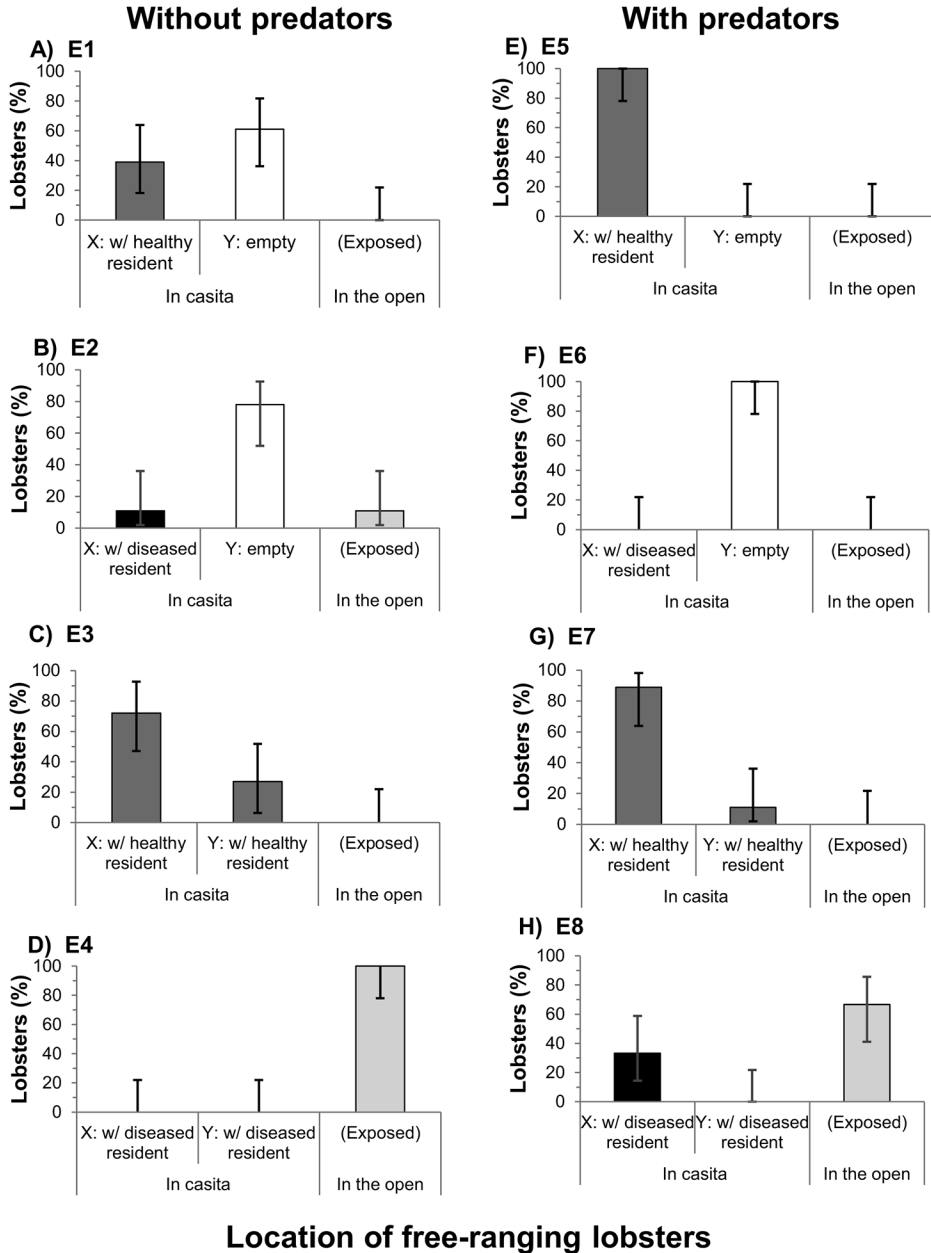


Figure 2. Results of experiments testing the shelter choice of groups of healthy, free-ranging *Panulirus argus* lobsters ($n = 18$ per experiment); (A–D) experiments E1 to E4, without predators (E–H) experiments E5 to E8, with predators. In E1 and E5 (A, E), casita X harbored a healthy resident (tethered lobster) and casita Y was empty; in E2 and E6 (B, F), casita X harbored a diseased resident and casita Y was empty; in E3 and E6 (C, G) both casitas (X and Y) harbored a healthy resident, and in E4 and E8 (D, H) both casitas harbored a diseased resident. Columns denote the percentages of lobsters that chose casitas with healthy residents (dark gray), casitas with diseased residents (black), empty casitas (white), and lobsters that remain exposed in the open (light gray). Error bars are 95% confidence intervals.

Table 2. Results of individual Fisher-Freeman-Halton exact tests comparing the shelter choice of groups of healthy free-ranging lobsters between pairs of experiments differing in the absence vs presence of (1) diseased resident lobsters, (2) alternate shelter (empty casita), or (3) predation risk.

Experiments	<i>P</i>
Absence vs presence of diseased residents	
E1 vs E2	0.069
E3 vs E4	<0.001
E5 vs E6	<0.001
E7 vs E8	<0.001
Absence vs presence of alternate shelter	
E1 vs E3	0.093
E2 vs E4	<0.001
E5 vs E7	0.486
E6 vs E8	<0.001
Absence vs presence of predation risk	
E1 vs E5	<0.001
E2 vs E6	0.052
E3 vs E7	0.402
E4 vs E8	0.019

the open and 10% sharing the casita with the diseased resident (Fig. 2B). In E3, with the two casitas harboring a healthy resident each, free-ranging lobsters used both, but one more than the other (70% and 30%), and none remained in the open (Fig. 2C). In contrast, when both casitas harbored a diseased resident (E4), all free-ranging lobsters (100%) were found in the open (Fig. 2D).

Experiments with Predators (E5–E8).—With a predatory triggerfish present, all free-ranging lobsters shared the casita with the healthy resident in E5 (Fig. 2E), whereas in E6, with one casita harboring a diseased resident and the other casita empty, all free-ranging lobsters used the empty casita (Fig. 2F). When the two casitas had a healthy resident (E7), more free-ranging lobsters aggregated in one of them (90%) and the rest (10%) in the other one, but none remained in the open (Fig. 2G). However, with both casitas harboring a diseased resident (E8), free-ranging lobsters either remained in the open (66.6%) or shared one casita with a diseased resident (33.3%) (Fig. 2H).

Comparisons between Experiments.—Table 2 provides the *P*-values from all Fisher-Freeman-Halton tests (2×3 contingency tables) comparing results of experiments. The first block corresponds to the four pairs of experiments in which the main difference was the absence vs presence of diseased residents. The results of E1 vs E2 did not differ significantly as most free-ranging lobsters grouped in the empty casita in both experiments, although in E1, some shared the casita with a healthy resident (Fig. 2A), whereas in E2, a few either shared the casita with a diseased resident or remained exposed (Fig. 2B). In the other three pairs of experiments, the difference was significant. In E3, lobsters shared the two casitas with healthy residents and none remained in the open (Fig. 2C), but in E4, with both casitas harboring diseased residents, all lobsters remained in the open (Fig. 2D). In E5, in the presence of a predator, all lobsters shared the casita with a healthy resident (Fig. 2E), whereas in E6, all lobsters aggregated in the empty casita, away from the diseased resident (Fig. 2F). Finally, in E7,

most lobsters grouped in one of the casitas with a healthy resident (Fig. 2G), whereas in E8, one third of the lobsters shared one of the casitas with a diseased resident while two thirds remained in the open (Fig. 2H).

The second block in Table 2 compares results between pairs of experiments in which the main difference was the absence vs presence of alternate shelter (an empty casita). The shelter choice of lobsters did not differ significantly between E1 (Fig. 2A) and E3 (Fig. 2C) or between E5 (Fig. 2E) and E7 (Fig. 2G). In E1 and E3, lobsters used both casitas regardless of whether only one (E1) or both (E3) harbored a healthy resident. In E5, all lobsters shared the casita with a healthy resident, and in E7, most lobsters shared one of the two casitas with a healthy resident, with only two using the other casita. In contrast, the difference was significant between E2, where most lobsters chose the empty casita (Fig. 2B), and E4, where all lobsters remained exposed rather than sharing either casita with a diseased resident (Fig. 2D), and also between E6, where all lobsters grouped in the empty casita (Fig. 2F), and E8, where some lobsters were found in the open, but some shared one of the casitas with a diseased resident (Fig. 2H).

The third block in Table 2 compares pairs of experiments in which the main difference was the absence vs presence of a predator. The difference was significant between E1 and E5, in which one casita held a healthy resident and the other was empty, because free-ranging lobsters indistinctly used both casitas in the absence of a predator (E1) (Fig. 2A), but all shared the casita with the healthy resident in the presence of a predator (E5) (Fig. 2E). When one casita held a diseased resident and the other was empty, the choice of shelter of free-ranging lobsters did not significantly differ between E2 (Fig. 2B) and E6 (Fig. 2F), although in the latter all lobsters chose the empty casita and none remained in the open (Fig. 2F). When the two casitas harbored a healthy resident, the shelter choice of lobsters was similar without (E3) or with a predator (E7), with lobsters preferentially using one of the two casitas and none exposed (Fig. 2C, G). Finally, when both casitas harbored a diseased resident, the shelter choice of free-ranging lobsters differed significantly, as all lobsters remained in the open in the absence of a predator (E4, Fig. 2D), but one third shared a casita with a diseased resident and two thirds remained exposed in the presence of a predator (E8, Fig. 2H).

REEF LAGOON CASITAS

Between January 2013 and May 2015, we conducted nine surveys totaling 450 casita recordings (50 casitas \times 9 surveys). Diseased and healthy lobsters were cohabiting in 181 casitas (40% of the total), and in 148, we were able to record the relative position of the diseased lobsters. In these 148 casitas, the total number of lobsters per casita varied from 2 to 29, but most (49%) had between 3 and 6. The mean lobster size differed significantly between diseased [mean: 25.2 (SE 0.59), range: 10–62 mm CL] and healthy lobsters [28.3 (SE 0.37), range: 9–76 mm CL] (Student's *t*-test, $t_{1260} = 3.812$, $P < 0.001$).

Diseased lobsters were segregated from healthy lobsters in 69 of the 148 co-occupied casitas (46.4%) and together with healthy lobsters in 79 (53.4%). When only two lobsters were present—one diseased and one healthy ($n = 22$ casitas)—significantly more casitas had lobsters that were segregated rather than together. However, this pattern tended to shift with increasing number of lobsters per casita, so that significantly more casitas had diseased and healthy lobsters that were together rather than

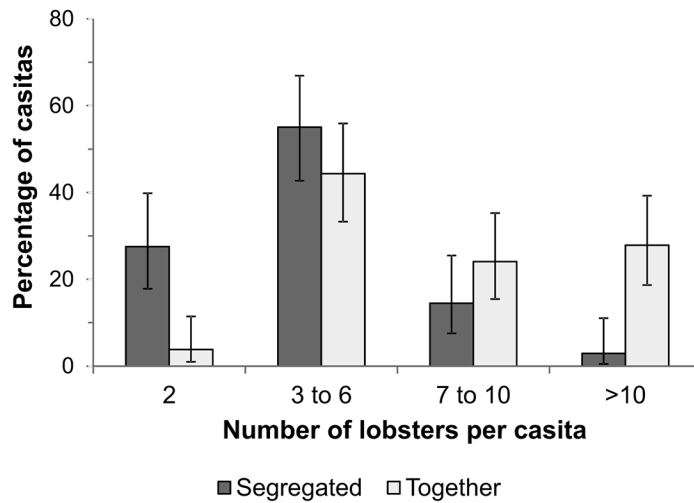


Figure 3. Distribution of *Panulirus argus* lobsters among 148 casitas co-occupied by diseased and healthy lobsters in the Puerto Morelos reef lagoon in which the diseased lobsters were apart from ($n = 69$ casitas) or together with ($n = 79$ casitas) healthy conspecifics. Error bars are 95% confidence intervals.

segregated when there were more than 10 lobsters ($n = 24$ casitas) (Fig. 3). However, the position of diseased lobsters relative to healthy lobsters did not differ significantly from random in casitas with 3–6 lobsters ($n = 73$) or with 7–10 lobsters ($n = 29$) (Fig. 3). The logistic regression analysis confirmed that, compared with the random position of diseased lobsters in casitas with 7–10 lobsters (reference level), the probability of finding diseased lobsters segregated from healthy conspecifics did not differ in casitas with 3–6 lobsters (odds ratio: 1.43), but was significantly higher in casitas with only 2 lobsters (odds ratio: 8.36) and significantly lower in casitas with more than 10 lobsters (odds ratio: 0.12) (Table 3). It should be noted that, although most of the 126 casitas with more than 3 lobsters had either one or two diseased lobsters (49.2% and 32.5%, respectively), some had 3 (12.7%), 4 (1.6%), or 5 (4.0%) diseased lobsters cohabiting with healthy conspecifics.

Many other conspicuous animal taxa, including potential predators, also were found in 111 (75%) of the casitas co-occupied by healthy and diseased lobsters. Some of these taxa were typically present as one to five individuals per casita, e.g., yellow stingrays [*Urobatis jamaicensis* (Cuvier, 1816)], spotted and purplemouth moray eels [*Gymnothorax moringa* (Cuvier, 1829) and *Gymnothorax vicinus* (Castelnau, 1825), respectively], queen triggerfish (*B. vetula*), groupers [*Epinephelus adscensionis* (Osbeck, 1765), *Epinephelus guttatus* (Linnaeus, 1758), *Epinephelus morio* (Valenciennes, 1828)], slipper lobsters [*Scyllarides aequinoctialis* (Lund, 1793)], banded shrimps [*Stenopus hispidus* (Olivier, 1811)], portunid crabs (e.g., *Achelous sebae* (H. Milne Edwards, 1834)], channel crabs [*Maguimithrax spinosissimus* (Lamarck, 1818)], spider crabs (*Mithraculus* spp.), and gastropods [e.g., *Fasciolaria tulipa* (Linnaeus, 1758), *Cypraea* spp.], but others were more commonly found in larger numbers, e.g., juvenile grunts (Haemulidae), several species of hermit crabs (Diogenidae and Paguridae), and some gastropods (Cerithiidae) and sea cucumbers (Holothuroidea).

Table 3. Estimates for logistic regression analysis testing the effect of the number of lobsters per casita (with four levels: 2 lobsters, 3–6 lobsters, 7–10 lobsters, more than 10 lobsters) on the probability of finding diseased lobsters segregated from (as opposed to together with) healthy lobsters cohabiting in casitas. The reference level was 7–10 lobsters.

Effect	Estimate	SE	Wald statistic	df	<i>P</i>	Odds ratio (95% CI)
Intercept	-0.278	0.267	1.085	1	0.297	
Lobsters per casita						
2 lobsters	2.124	0.514	17.074	1	<0.001	8.36 (3.05, 22.90)
3–6 lobsters	0.360	0.314	1.315	1	0.251	1.43 (0.77, 2.65)
More than 10 lobsters	-2.120	0.586	13.069	1	<0.001	0.12 (0.04, 0.38)

DISCUSSION

We tested two hypotheses related to the shelter choice of free-ranging healthy *P. argus* juveniles in the presence/absence of diseased conspecifics, alternate shelter, and predation risk. Previous laboratory studies examining disease avoidance by healthy lobsters used a single test lobster per trial and either did not include predators (Behringer et al. 2006) or included a restrained predator that was visually and chemically perceived by lobsters (Behringer and Butler 2010). In both studies, most lobsters preferred an empty shelter over a shelter with a diseased conspecific, thus foregoing the protection of group defense in favor of reduced infection risk (Behringer and Butler 2010). However, our experiments differed from those studies in that we used groups of healthy lobsters as opposed to individual healthy lobsters, casitas (low-lying shelters that can accommodate multiple lobsters) as opposed to smaller individual shelters, and an unrestrained predator, translating into a more immediate risk of predation.

In our experiments without predators, free-ranging lobsters generally avoided casitas with diseased resident lobsters, so much so that in E4, with both casitas harboring a diseased resident, all free-ranging lobsters in all replicate tanks remained in the open rather than using either casita. These results demonstrate a strong expression of disease avoidance behavior, as reported in other laboratory studies (e.g. Behringer et al. 2006, Behringer and Butler 2010, Anderson and Behringer 2013, Candia-Zulbarán et al. 2015), and confirm that, given the option, most healthy juvenile *P. argus* would choose to not cohabit with PaV1-diseased conspecifics. They also corroborate that these lobsters can rapidly assess the absence of predation risk and modify their behavior accordingly (Lozano-Álvarez 1996, Lozano-Álvarez and Spanier 1997), for example, remaining in the open during the day. However, there was an exception: in one of the replicate trials of E2, two free-ranging lobsters were found in the open and two chose the casita with a diseased resident. This particular trial (which caused the heterogeneity test for E2 to be significant) suggests that, even in the absence of predation risk, some lobsters may choose to cohabit with diseased lobsters. However, although the clinical signs of all diseased lobsters used in our experiments suggest that they were in grades 2 and 3 in Li et al.'s (2008) scale of infection severity from 0 (no infection) to 3 (severely infected) (Cruz-Quintana et al. 2011), it is unknown whether healthy lobsters are able to assess the severity of the disease in diseased conspecifics.

The risk of predation in our experiments greatly affected the casita choice of lobsters in the presence of diseased conspecifics, further modulated by availability of

alternate shelter. Thus, with a triggerfish present and only one of the two available casitas harboring a diseased resident (E6), all free-ranging lobsters in all replicates aggregated in the alternate, empty casita, but with both casitas harboring diseased residents (E8), some lobsters were found in the open and some shared a casita with a diseased conspecific. In E8, the exposed lobsters were observed to be alert, in close contact with each other as the fish roamed the tank, raising and moving their long, spiny antennae together when the fish approached. This collective defense behavior is well documented in *P. argus* (Herrnkind et al. 2001, Briones-Fourzán et al. 2006). Interestingly, in those trials of E2 and E8 in which some lobsters chose a casita with a diseased resident, they were observed in the entrance opposite to that to which the diseased resident was tethered.

In the reef lagoon, by contrast, healthy and diseased lobsters were found cohabiting in 40% of the casitas surveyed, a level similar to that found by Briones-Fourzán et al. (2012) in commercial casitas distributed over a bay zone in Bahía de la Ascensión (38%) similar to the Puerto Morelos reef lagoon. The casitas that we used in this reef lagoon were smaller than commercial casitas, but still provided a substantially larger (1.2 m²) shelter area than the casitas used in the tanks (0.18 m²), allowing for greater aggregations of lobsters. In shelter-poor habitats, casitas also provide refuge for numerous other taxa (e.g., Mintz et al. 1994, Sosa-Cordero et al. 1998, Cruz and Phillips 2000, Briones-Fourzán et al. 2012, present study), reducing competition for shelter and allowing cohabitation of lobsters with other taxa (Lozano-Álvarez et al. 2010), including predators, which do not usually attack lobsters inside a casita because the limited height constrains their movements (Lozano-Álvarez and Spanier 1997). However, the co-occurrence of this multiple and varied fauna may increase the background chemical noise in a casita, potentially creating a dynamic pattern of chemical signals and noise (Atema 2012). It is unknown whether or to what extent chemical noise can mask the signal of a diseased lobster, but the release of odors in *P. argus* is size-dependent (Ratchford and Eggleston 1998) and about 60% of the diseased lobsters found in our casitas were <30 mm CL. The extent of the dispersal field of the chemical signal produced by a diseased lobster may also be influenced by flow speed and turbulence (Finelli 2000, Atema 2012, Anderson and Behringer 2013), but in shelter-poor areas with an elevated risk of predation, lobsters seeking refuge may have to decide quickly whether or not to take shelter in a given casita. In other animals, quick decisions in most sensory tasks often come at the expense of accuracy, particularly for stimuli that are difficult to identify (Kay et al. 2006).

Because lobsters are not static within a casita, our results on the relative location of diseased vs healthy lobsters provide only a snapshot of their potential use of the casita space. However, it is interesting that the probability of finding diseased lobsters segregated from healthy lobsters decreased with increasing number of lobsters in the casita. In casitas co-occupied by only one healthy and one diseased lobster, the former probably tries to keep some distance from the latter, but this may become more difficult to accomplish as more lobsters gather in the casita, especially with more than one diseased lobster in that casita. Because diseased lobsters retain their gregarious behavior (Behringer and Butler 2010), they may attempt to aggregate with healthy conspecifics, resulting in a similar probability of being apart vs together at the time we surveyed casitas with up to 10 lobsters, but with more and more lobsters, the chances of finding diseased lobsters segregated drastically decreased. Therefore, the large shelter area of casitas does allow for segregation of healthy and diseased

lobsters, but only to a certain point, depending on the number of lobsters using a given casita at a given time and the gregarious behavior expressed by the diseased lobsters.

Results of the present study confirm that, in general, healthy *P. argus* lobsters express behavior immunity by avoiding shelters harboring diseased conspecifics. However, it is important to note that, in our laboratory experiments, not all healthy lobsters avoided casitas with diseased conspecifics. This has also been the case in studies conducted by other authors. Thus, in the shelter choice experiments conducted by Behringer et al. (2006) and Behringer and Butler (2010) in mesocosmos, about 20% of all healthy focal lobsters did not avoid shelters harboring diseased conspecifics. In shelter choice experiments conducted in Y-mazes, about 20% of the healthy focal lobsters chose shelters emanating chemical scents of diseased lobsters over shelters emanating plain seawater (Anderson and Behringer 2013, Candia-Zulbarán et al. 2015). Similarly, when Florida traps were baited with live healthy vs diseased lobsters to examine their effects on free healthy lobsters, not all healthy lobsters avoided traps containing diseased lobsters (Behringer et al. 2012), and in the field experiment of Butler et al. (2015), not all lobsters left the natural shelters to which a diseased lobster was added.

Overall, these results likely reflect either natural variation in the personality traits related to antipredator defenses and behavioral immunity among conspecifics (Pike et al. 2008, Wolf and Weissing 2012), the expression of which can further depend on ecological contexts (Sih et al. 2004), or that the lobsters we used in our experiments may have had different experiences with predators such that some individuals might be more risk averse, while others might be less so (Stankowich and Blumstein 2005). The fitness of individuals lies at the heart of ecological theories, and both predation and the risk of disease are major forces determining the fitness of individuals (Hart 1990, Lima and Dill 1990). It should be advantageous to be able to effectively detect high predation risk and behave accordingly to reduce successful predation (Hazlett 2011), but given that predation risk may vary greatly over different ecological contexts or temporal scales, the antipredator adaptations of an individual should be sensitive to the current level of predation risk to be able to realize more in its lifetime than simply avoiding predation (Lima and Dill 1990). Similarly, defenses against pathogens, including behavioral immunity (i.e., disease avoidance, which is akin to “disgust sensitivity,” Curtis et al. 2011), may reduce the risk of disease, but just as there are benefits and costs of antipredator responses (Lima and Dill 1990), there are benefits and costs of immunity responses (McKean and Lazzaro 2011). Therefore, it may be advantageous for individuals to be able to regulate their disgust sensitivity according to their current physiological state or ecological context, that is, increasing it under certain circumstances (e.g., when its vulnerability to pathogens is high), or lowering it under others (e.g., when it perceives a high risk of predation) (Curtis et al. 2011, Schaller and Park 2011).

In summary, for a shelter-seeking spiny lobster, there will be a conflict in deciding whether or not to share a shelter with a diseased conspecific. This conflict must be resolved based upon the lobster’s assessment of the current risk of predation, its prior experience with predators (and disease), and the costs and benefits associated with its behavioral options. Indeed, high-fitness individuals are not necessarily those possessing the greatest pathogen defense or the greatest antipredator defenses, but those making the best compromise between the competing needs for surviving to

achieve reproductive success (McKean and Lazzaro 2011). The trade-offs made by *P. argus* in the face of multiple threats reflect the complex behavior of this species and its flexibility under different ecological contexts.

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