

Disease avoidance influences shelter use and predation in Caribbean spiny lobster

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Abstract Shelter competition is uncommon among social animals, as is the case among normally gregarious Caribbean spiny lobsters (*Panulirus argus*). However, healthy lobsters avoid sheltering with conspecifics infected by a lethal pathogenic virus, PaV1. These contradictory behaviors have implications for shelter use and survival, especially in areas where shelter is limited. In laboratory experiments, we tested shelter competition between paired healthy and diseased juvenile lobsters in shelter-limited mesocosms. Neither healthy nor diseased lobsters dominated access to shelters, but lobsters shared shelter less often when diseased lobsters were present relative to controls with two healthy lobsters. We hypothesized that exclusion of juvenile lobsters from shelter results in increased mortality from predation, especially for the more lethargic, infected individuals. Field tethering trials revealed that predation was indeed higher on infected individuals and on all tethered lobsters deprived of shelter. We then tested in mesocosm experiments how the contrasting risks of predation versus infection by a lethal pathogen influence shelter use. Lobsters were offered a choice of an empty shelter or one containing a diseased lobster in the presence of a predator (i.e., caged octopus) whose presence normally elicits shelter-seeking behavior, and these data were compared with a previous study where the predator was

absent. Lobsters selected the empty shelter significantly more often despite the threat of predation, foregoing the protection of group defense in favor of reduced infection risk. These results offer striking evidence of how pathogenic diseases shape not only the behavior of social animals but also their use of shelters and risk of predation.

Keywords PaV1 · Infection risk · Virus · Shelter limitation · *Panulirus argus* · Competition

Introduction

Refuges that provide protection from predators are a resource for which competition is particularly acute, given the often mortal consequences of scarce shelter (Söderbäck 1994). Shelter limitation leads to the emergence of competitively dominant species, successful species invasions, or interference competition among members of the same species, as has been demonstrated in freshwater crayfish and coral reef fish (Butler and Stein 1985; Hixon and Beets 1993; Söderbäck 1994; Steele 1999; Vorburger and Ribi 1999; Holbrook and Schmitt 2002; Fero and Moore 2008). Exclusion of the inferior competitor from shelter often results in increased predation, giving further advantage to the dominant species or individuals. Although shelter competition is potentially a strong selective force for nonsocial species, the situation for social species is decidedly different. The evolution of sociality and cooperation is theorized to repress competition for limited resources such as shelter (Frank 2003).

Some social species, such as spiny lobsters, minimize shelter competition and indeed capitalize on communal living by sharing shelters to decrease the risk of predation due to increased vigilance or group defense (Pulliam 1973;

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Herrnkind 1980; Foster and Treherne 1981; Butler et al. 1999; Dolan and Butler 2006). However, sociality incurs tradeoffs. Benefits to social species include increased efficiency of resource exploitation (Childress and Herrnkind 2001), strengthened immune function (Lutermann and Bennett 2008), and reduced predation (Dolan and Butler 2006), whereas potential costs include increased prevalence of disease (Hughes et al. 2002), decreased genetic diversity (Hughes and Boomsma 2004), and local resource depletion (Schaffer et al. 1979). Spiny lobsters of the family Palinuridae all display some level of sociality, and the Caribbean spiny lobster *Panulirus argus* is particularly gregarious, although the pattern of sociality and the availability of shelter for *P. argus* changes in lockstep with ontogeny (see Childress 2007 for review).

The complex life cycle of *P. argus* includes an open-ocean planktonic larval stage of unknown sociality, an asocial early benthic juvenile (EBJ) stage that dwells in vegetated habitats, a social crevice-dwelling juvenile stage, and a social reef-dwelling adult stage. Following a prolonged larval and postlarval period of several months (Goldstein et al. 2008), *P. argus* begins its benthic existence as a cryptic, asocial EBJ that lives for several months within structurally complex, vegetated settlement habitats (e.g., macroalgae, seagrass, mangrove prop roots) (Marx and Herrnkind 1985; Herrnkind and Butler 1986; Herrnkind et al. 1988; Behringer et al. 2009). At approximately 15–25 mm carapace length, the EBJ undergo an ontogenetic shift in behavior, coloration, habitat use, and susceptibility to a lethal, pathogenic virus (PaV1). Emerging from their settlement habitat, the EBJ begin to seek shelter in crevices provided by sponges, corals, and rocks and gradually lose their camouflage coloration (Marx and Herrnkind 1985). At this time, they also become social and are attracted to conspecifics (Ratchford and Eggleston 1998; Childress and Herrnkind 2001), although up to 40% of the juveniles still dwell alone in dens (Behringer et al. 2006). The gregarious nature of spiny lobsters does not result in density-dependent depletion of their nutritional condition nor increased emigration/mortality (Behringer and Butler 2006). Despite the lack of density-dependent intraspecific interactions among juvenile lobsters, the availability of crevice shelters for them is viewed as a potential demographic bottleneck (Butler and Herrnkind 1997). Shelter limitation is further exacerbated when catastrophic events, such as harmful algal blooms, periodically decimate crevice-providing sponge communities in large portions of the Florida Keys nursery (Butler et al. 1995; Herrnkind et al. 1997; Stevely and Sweat 1998; Peterson et al. 2007). In Florida, large structure-forming sponges are the primary shelter for juvenile lobsters, and their loss impacts the distribution, aggregation, and survival of juvenile lobsters—the loss of sponge shelters may even alter disease dynamics in *P. argus* populations.

Caribbean spiny lobsters are plagued by PaV1 and their susceptibility to the virus changes with ontogeny: infection prevalence is inversely related to lobster size (Shields and Behringer 2004). Local prevalence can reach 30% among juveniles in nursery areas in Florida and Mexico, although mean prevalence is typically between 5% and 7% (Shields and Behringer 2004; Behringer 2003; Lozano-Álvarez et al. 2008). PaV1 is transmitted via contact and ingestion of infected tissue (e.g., cannibalism) and—among the smallest juveniles (<20 mm CL)—over short distances through the water (Butler et al. 2008). Faced with this lethal pathogen, *P. argus* has developed a behavior that contrasts with their normally gregarious behavior. Healthy lobsters can detect and avoid lobsters infected with PaV1 and do so before the infected individual becomes infectious, potentially reducing the risk of infection by contact transmission (Behringer et al. 2006; Butler et al. 2008). In the wild, this results in the nearly complete isolation of infected individuals (~90%). Aggregation with conspecifics in shelter-limited habitats is clearly complicated by the need to avoid potential infection by PaV1. Appropriately sized shelter (Hixon and Beets 1993; Eggleston et al. 1990; Eggleston and Lipcius 1992) and aggregation with conspecifics in those shelters (Herrnkind 1980; Mintz et al. 1994; Dolan and Butler 2006) protects small lobsters from predators, so adequate shelter is crucial for juvenile spiny lobster survival.

PaV1 is not the only threat to survival for juvenile *P. argus*. Juvenile lobsters face a diverse array of predators including snappers, groupers, sharks, rays, crabs, and octopus (Smith and Herrnkind 1992; Weiss et al. 2008). Diseased individuals in the late stages of infection are lethargic and dwell alone, which may increase their susceptibility to predators. Indeed, the consumption of sick (Hudson et al. 1992; Lefcort and Blaustein 1995; Ives and Murray 1997; Alzaga et al. 2008) or weakened (Møller and Erritzøe 2000; Murray 2002) individuals by predators is a common theme in predator–prey dynamics. Although often difficult to test empirically (Temple 1987), removal of disease-compromised individuals may facilitate greater population health by selecting for individuals with greater fitness (Møller and Erritzøe 2000) or by removing infected individuals that contribute to the spread of disease (Ostfeld and Holt 2004). Spiny lobsters are not without antipredatory adaptations and are capable of detecting and avoiding certain types of predators, such as octopus (Berger and Butler 2001). Thus, tradeoffs in shelter choice may occur in shelter-limited habitats where both diseased conspecifics and predators are present. However, tradeoffs and shelter competition would not be expected between healthy lobsters, which gain the benefit of group defense without the cost of infection.

Our objective in this study was to investigate the impacts of disease on shelter use and predation in a social organism,

the Caribbean spiny lobster. We employed a series of manipulative experiments to: (1) determine if shelter competition occurs between healthy and diseased lobsters, (2) test whether healthy and diseased lobsters differ in their susceptibility to predation and if shelter exclusion is more costly to one or the other, and (3) examine the potential tradeoff between the risks of predation and infection when shelter is limited.

Methods

All field experiments were conducted from June–August 2008, in shallow hard-bottom habitat 2–3 km north of Long Key in the middle Florida Keys (USA). The laboratory experiments took place during the summers of 2007, 2008, and 2009 at the Goshen Marine Laboratory in the Florida Keys. Although PaV1 appears to be a ubiquitous disease in lobsters in the Florida Keys and elsewhere in the Caribbean (Butler et al. 2008; Lozano-Álvarez et al. 2008), we took precaution to prevent its further spread. All wastewater from laboratory experiments was sterilized with UV to kill PaV1 and prevent contamination. Also, diseased lobsters used in field experiments were all captured in the surrounding habitat so as not to introduce additional disease individuals into the region.

Shelter competition

This experiment took place in 420-L seawater-filled static tanks with aeration and a single concrete brick shelter (Fig. 1a). Each trial was 24 h long and initiated during the

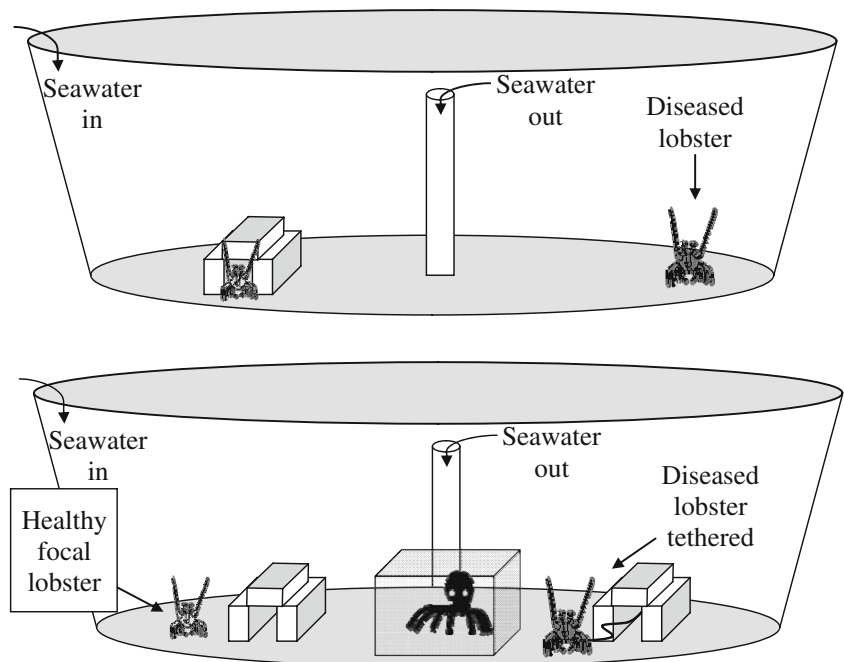
day, when lobsters normally reside within shelters. The final shelter residents were determined during daylight 24 h later. This provided them a full night of activity after which they normally seek shelter. All healthy lobsters used in these trials were juveniles (20–50 mm carapace length, CL) captured from the field and had not been previously exposed to infected lobsters in the laboratory. Once exposed, they were not reused in experiments nor were they released back into the wild. Antennae tags permitted us to identify individuals in each trial.

We tested one healthy and one diseased lobster or two healthy lobsters (control) with only one shelter available. To determine if initial residency of the shelter affected the final resident outcome, we randomly introduced one lobster 2 h before the other. The experiment consisted of three treatments: (1) a healthy lobster introduced first and then a diseased lobster (HD), (2) a diseased lobster introduced first and then a healthy lobster (DH), and (3) a healthy lobster introduced and then another healthy lobster (HH—control). The patterns of shelter use by lobsters relative to the treatment type were evaluated using contingency table analyses.

Relative predation susceptibility

To determine the relative susceptibility to predation of diseased and healthy lobsters, we tethered lobsters in hard-bottom areas with similar characteristics to minimize confounding differences in predators or habitat (Peterson and Black 1994; Mills et al. 2008). Hard-bottom habitat consists of a flat limestone substrate covered by a thin layer (approximately 1–5 cm) of sediment. Conspicuous sessile

Fig. 1 Diagrams of mesocosms used for **a** the shelter competition experiment and **b** to test shelter selection among lobsters given the choice between an empty shelter and a shelter with a diseased lobster in the presence of a lobster predator (octopus)



organisms in this habitat include abundant and large (0.25–1.0 m) sponges such as the vase sponge (*Ircinia campana*) and loggerhead sponge (*Sphaciospongia vesparium*), coral heads such as star corals (*Solenastrea hyades* and *Siderastrea sideria*), and numerous gorgonians such as sea plumes (*Pseudopterogorgia* spp.) and sea whips (*Pterogorgia* spp.). Undercuts and holes in large sponges and coral heads, in combination with numerous solution holes in the substrate, provide the primary shelters for lobsters. Tethering trials took place in July and August 2008 in three shallow hard-bottom sites north of Long Key, FL where natural shelter densities were similar.

We conducted two types of tethering experiments: one in which healthy and diseased lobsters were tethered in the open, and a second where lobsters were tethered near natural shelters (e.g., sponges, coral heads, and solution holes). Healthy and diseased lobsters (17–52 mm CL) were collected from the surrounding region and, prior to tethering, their size (CL), sex, and disease status recorded. Only lobsters with visible (i.e., late stage) PaV1 infections were used. Infected lobsters were identified by observing the color of the hemolymph through the dorsal juncture between the cephalothorax and abdomen. Healthy lobsters have clear hemolymph whereas lobsters visibly infected with PaV1 have chalky-white hemolymph (Shields and Behringer 2004). A monofilament harness with a snap swivel was then fitted around each lobster, which then was attached to a concrete brick anchor by a 25-cm long monofilament line. This length of monofilament allowed limited movement but prevented entanglement.

For the first experiment, the tethered lobsters ($n=60$ healthy and 14 diseased) were then haphazardly selected and placed on the seafloor in the open 3.5 m apart at positions marked along a transect tape. The disparity in replicates for each treatment is due to the limited availability of diseased lobsters and our reticence to introduce diseased lobsters from surrounding areas. In the second tethering experiment, we assessed the impact of shelter on the relative predation rate of diseased and healthy lobsters by tethering lobsters ($n=22$ diseased and 24 healthy) next to naturally occurring shelters (i.e., sponges, coral head, solution hole) rather than in the open along a transect line. In both the non-shelter and shelter trials, the status of the lobsters (present, absent) was checked by divers after 24 and 48 h. Predatory attacks usually resulted in a severed tether or carapace remains still attached. Any healthy lobsters that remained alive at the experiment's conclusion were released, whereas diseased lobsters were returned to the laboratory and never released in the wild.

Predator effect on avoidance behavior

We previously confirmed in a laboratory experiment, in which lobsters were offered a choice of sheltering alone or

with a diseased lobster, that healthy lobsters rarely cohabitate with a diseased conspecific (14% of trials) and instead shelter alone (86% of trials; Behringer et al. 2006). Here, we repeated the experiment in exactly the same way but with an octopus present to assess the tradeoff between cohabitation with a diseased conspecific or sheltering alone without the benefit of group defense.

This experiment took place in 420-L flow-through seawater mesocosms containing two concrete brick shelters situated 1 m apart (Fig. 1b). To one of the shelters, we tethered a PaV1-infected lobster, and the other shelter was left open. Between the two shelters, we placed a clear, perforated plastic container (20×40×10 cm) containing an octopus (*Octopus briarius*)—a known lobster predator (Berger and Butler 2001; Butler and Lear 2009). An air stone inside the container supplied oxygen to the octopus and circulated water and octopus odors out of the container. In the afternoon of each day, we recorded the CL and sex of a healthy lobster and released it into the mesocosm. After 24 h, we recorded its shelter choice (empty den vs. den with diseased conspecific). The octopus was replaced every 2 to 3 days.

Statistical methods

Shelter competition We used a 3×4 contingency table analysis to test the independence among the three treatments (DH, HD, and HH control) and four possible outcomes: (1) the lobster initially resident in shelter was the final shelter resident, (2) the second introduced lobster was the final shelter resident, (3) both lobsters shared the shelter, or (4) neither lobster was within the shelter.

Relative predation susceptibility We used a 2×2×2 log-linear model to determine if the survival of tethered lobsters (presence or absence after 24 h) depended on their health status (diseased or healthy) and shelter use (shelter or no shelter).

Predator effect on avoidance behavior We used a binomial test to determine if the proportion of healthy lobsters that selected the empty shelter while in the presence of an octopus differed from that predicted by results from a previous experiment in which no octopus was present (p (alone)=0.86).

Results

Shelter competition

The pattern of shelter occupancy differed significantly among the four trial outcomes (Likelihood Ratio $\chi^2=$

23.6749, $df=6$, $P=0.0006$) (Fig. 2). There was no statistical difference between the DH and HD trials (Likelihood Ratio $\chi^2=4.274$, $df=3$, $P=0.2334$), which are logically identical (i.e., one diseased and one healthy lobster present) for testing the hypothesis of interest, so we combined these two trials for comparison to the control where two healthy lobsters were present (HH). The presence of a diseased lobster (DH+HD) resulted in a significantly different pattern in shelter occupancy compared to the control (HH) (Likelihood ratio $\chi^2=19.40$, $df=3$, $P=0.0002$).

There was no clear competitive superiority by either healthy or diseased lobsters for the single available shelter. Therefore, we refocused a second analysis on the most ecologically relevant result of shelter competition—the frequency of exclusion from shelter when a diseased lobster is present (DH+HD treatments) or not (HH treatment). The trial outcomes were simply reclassified into “co-occupation” versus “exclusion” (i.e., one or both lobsters excluded) and reanalyzed using a Fisher’s exact test. The test was significant ($df=1$, $P=0.0041$) indicating that when a diseased lobster was present, there was a greater chance that either one of both lobsters would be excluded from shelter (Fig. 3).

We frequently observed lobster behavior directly during portions of each trial and periodically videotaped (under infrared illumination) the trials at night. When healthy and diseased lobsters were tested, it appeared that a combination of avoidance of diseased lobsters by healthy lobsters and pursuit of shelter or conspecifics (i.e., aggregative behavior) by diseased lobsters resulted in alternating occupation and abandonment of the shelter by each lobster. Thus, the health status of the final resident of a single

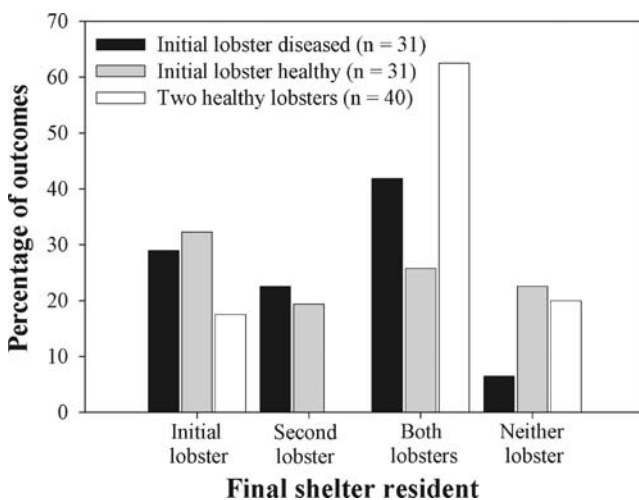


Fig. 2 Outcome of a shelter competition experiment in which the final residency of the single available shelter (x-axis) was either: the initial lobster introduced into the mesocosm, the second lobster introduced, both lobsters, or neither lobster. We compared treatments (histograms) where the initial resident was either healthy or diseased to controls where both lobsters were healthy

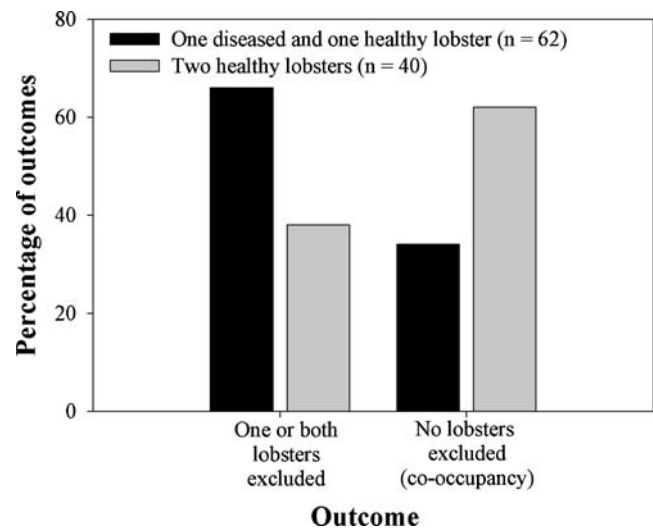


Fig. 3 Outcome of a shelter competition experiment in which: one or both lobsters were excluded from the shelter or they co-occupied the shelter (x-axis). We compared treatments (histograms) where one lobster was healthy and one diseased to controls where both lobsters were healthy. Significantly more trials resulted in exclusion when a diseased lobster was present, regardless of the order of introduction, compared to two healthy lobsters ($P=0.0041$)

shelter was equally probable and simply the one fortunate enough to be in the shelter the next day when we recorded the outcome. That was in contrast to the situation when two healthy lobsters were tested and consistently co-occupied the single available shelter.

Relative predation susceptibility

From the loglinear analysis of lobster susceptibility to predation in the field, we found no interaction between lobster health (diseased vs. healthy) and shelter access (tethered in shelter vs. tethered in the open) affecting survival ($G=1.174$; $df=1$; $P=0.278665$). However, two two-way interactions were significant, with both health status ($G=15.168$; $df=1$; $P=0.000098$) and shelter access ($G=3.840$; $df=1$; $P=0.050039$) significantly affecting lobster survival (Fig. 4). More diseased lobsters were killed by predators than healthy lobsters, and more lobsters died when tethered without access to shelter.

Predator effect on avoidance behavior

In a prior study (Behringer et al. 2006), healthy and diseased lobsters were tested separately and chose between sheltering alone or with a diseased lobster in the absence of a predator. We repeated that experiment but with the addition of an octopus predator to test if predation risk altered the result. Using the prior data to generate a null hypothesis for the current study, we found no difference in choice of shelter by

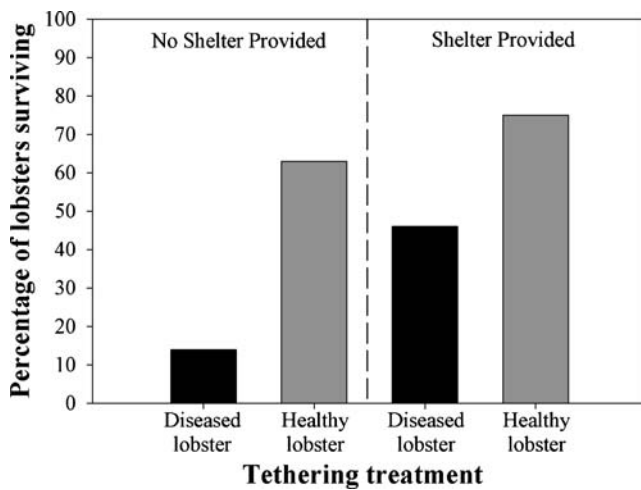


Fig. 4 Survival of healthy ($n=60$) and diseased ($n=14$) lobsters in field tethering experiment where shelter was not provided (left panel) and where lobsters ($n=22$ diseased and $n=24$ healthy) were tethered next to a sponge or coral head shelter (right panel). A greater proportion of healthy lobsters survived the 24 h trial compared to diseased lobsters ($P=0.000098$), and regardless of health status, more lobsters survived when shelter was available than when exposed in the open ($P=0.050039$)

healthy or diseased lobsters when octopus were present (Binomial test, $P=0.267$). As in the previous study, healthy lobsters preferred an empty shelter (20 trials) over one containing a diseased lobster (five trials) even when in the presence of a predator (Binomial test, $P=0.004$).

Discussion

The presence of PaV1 infection alters the normal behaviors of healthy and infected lobsters (Behringer et al. 2006, 2008), and in this study, we demonstrated that these changes indirectly effect lobster survival. Interference shelter competition between healthy and diseased lobsters resulted in increased exclusion from shelters, regardless of the health of the initial resident. Exclusion from shelter increases predation risk, which is high for small, vulnerable juvenile lobsters (Smith and Herrnkind 1992; Behringer et al. 2009) but even more so when they are infected by PaV1 as we demonstrated here. We found that the threat of disease trumped the risk of predation to healthy lobsters. Even when a predator (whose odors lobsters detect and normally avoid; Berger and Butler 2001) lurked nearby, the normally social, healthy lobsters still chose solitary habitation over cohabitation with a PaV1-infected lobster. Our results offer striking evidence of how pathogenic diseases can influence shelter use and risk of predation in social animals.

The availability of crevice shelters is a limiting resource for juvenile *P. argus* in many regions of the Caribbean and

can act as a bottleneck to future population size (Butler and Herrnkind 1997; Herrnkind et al. 1997; Briones-Fourzán et al. 2007). The social nature of *P. argus* normally ameliorates many of the potential negative density-dependent competitive effects one might expect when shelter is scarce (Behringer and Butler 2006; Dolan and Butler 2006). However, the aversion that healthy lobsters have toward PaV1-infected conspecifics (Behringer et al. 2006) can reestablish a role for shelter competition in the ecology of this social species if shelter is scarce. Disease-enhanced shelter competition is not only relevant in regions where shelter is naturally limiting (Eggleston et al. 1990; Butler and Herrnkind 1997; Lozano-Álvarez et al. 2008) but also where the availability of shelter is diminished by environmental degradation, as is the situation in the Florida Keys where our study took place.

In Florida, sponges are the primary shelter used by juvenile lobsters (Forcucci et al. 1994; Butler and Herrnkind 1997; Bertelsen et al. 2009), but in the past few decades, cyanobacteria blooms have caused mass sponge die-offs over approximately 25% of the nursery area, further reducing shelter availability for lobsters (Butler et al. 1995; Herrnkind et al. 1997). Healthy lobsters in these areas face the Faustian choice between sharing a den with a conspecific who harbors a fatal, transmissible disease or enduring the threat of predation alone in the open or, having driven a diseased lobster out of its shelter, alone in a den without the benefit of group defense. Predation on diseased lobsters, which already experience higher rates of predation, may also increase in sponge die-off areas if excluded from shelters by healthy lobsters. Yet, the diseased lobster is not always the loser when competing for shelter.

Diseased and healthy lobsters are equivalent competitors for shelter. However, the competition for shelter that ensues between diseased and healthy lobsters is a type of asymmetrical interference competition. Although the normally gregarious healthy lobsters avoid cohabitation with infected lobsters, infected lobsters do not lose their gregarious tendency and will co-occupy a shelter with either healthy or diseased conspecifics (Behringer et al. 2006). In nature, we expect that fewer interactions would occur between healthy and diseased lobsters over a single shelter as we suspect that the loser of that competitive interaction would move on to seek another shelter. However, this would not alter our findings that healthy and diseased lobsters are equal competitors and thus equally likely to occupy scarce dens in the wild.

Caribbean spiny lobsters fall prey to a multitude of predators so access to shelter is critical to lobster survival, especially when lobsters are small (Eggleston et al. 1990; Smith and Herrnkind 1992; Weiss et al. 2008). Lobsters respond to this threat by sheltering in aggregations for defense during the day (Butler et al. 1997), being nocturnal

to avoid most piscine predators, and by limiting the time and distance away from shelter spent foraging until they reach adulthood (Childress and Herrnkind 2001; Weiss et al. 2008). However, shelter competition resulting from the presence of diseased lobsters disrupts normal sheltering behavior in ways that potentially subject healthy and diseased lobsters to greater predation.

The results of our tethering experiments, although only a relative measure of predation, demonstrate the dire consequences of exposure for diseased lobsters, especially lobsters in the late stages of infection that are more sedentary and lethargic (Butler et al. 2008). The culling of weak or sick animals from a population is a common ecological paradigm theorized to increase population health by decreasing the spread of pathogens (Ostfeld and Holt 2004) or by removing substandard individuals from the population (Temple 1987). Higher rates of predation on diseased lobsters along with their isolation from healthy lobsters that avoid them may together depress the prevalence of PaV1 infection. Indeed, the prevalence of PaV1 infections in the Florida Keys has remained at 5–7% (Behringer and Butler unpublished data) since 1999, although its prevalence has increased in Mexico (Lozano-Álvarez et al. 2008). Based on the condition of the remains of many tethered individuals (i.e., completely dismembered but not masticated), we suspect that octopus (Berger and Butler 2001; Weiss et al. 2008) were partially responsible.

In nature, lobsters avoid shelters where octopuses reside and the spatial distribution of lobsters is strongly influenced by this behavior (Berger and Butler 2001). We initially hypothesized that the immediate risk of predation posed by an octopus would dictate shelter choice, overriding the long-term threat of mortality posed by contraction of the lethal PaV1 virus. However, when facing the imminent threat of predation, healthy lobsters did not co-occupy a shelter with a diseased lobster, depriving both healthy and diseased lobsters of the benefit of group defense (Mintz et al. 1994; Butler et al. 1997; Dolan and Butler 2006). Our tethering results suggest that the consequences of this are greater for diseased lobsters, which experienced greater predation relative to their healthy conspecifics, presumably because as the disease progresses in lobsters, it causes increasing lethargy (Butler et al. 2008).

A broader view of pathogen effects on host demographics

Pathogens can alter nearly all facets of host population dynamics (e.g., growth, movement, fecundity, mate choice, susceptibility to predation, survival) and thus can have strong effects on the demography of natural animal populations. A number of studies have shown that pathogens can disrupt species interactions such as competitive hierarchies and predator–prey relationships (Kiesecker

and Skelly 2001; Koprivnikar et al. 2008, Lefèvre et al. 2009). Parasitoid wasps and flies can affect host spatial distributions because they are highly mobile and activity search for hosts in a predator-like fashion. In such cases, aggregation by the host reduces the per capita probability of infection in both theoretical models and in field studies of ungulates (Mooring and Hart 1992) and stickleback fish (Poulin and Fitzgerald 1989). Pathogens may even regulate host population abundance and cycles (Hudson and Greenman 1998), with important consequences for the structure of animal communities (Sousa 1991; Marcogliese and Cone 1997; Thompson et al. 2005). Community structure may, in turn, influence the spread of infectious diseases. For example, Schmidt and Ostfeld (2001) modeled the spread of Lyme disease by ticks in mammalian communities of differing structure and found that the disease declined when host community richness increased and when the host species representing the most competent pathogen reservoir were community dominants.

Pathogens can also impact host demographics via their sometimes bizarre effects on the behavior of infected hosts. Aquatic examples include parasitic rhizocephalan barnacles that castrate and feminize male crabs, thus impacting crab reproductive dynamics (Reinhard 1950). Parasitic trematodes invade the nervous system of salt marsh killifish summoning conspicuous behaviors (e.g., surfacing, flashing, shimmying) in their host that result in higher rates of killifish predation by wading birds, thus completing the complex life cycle of the parasite (Lafferty and Morris 1996). A poorly explored area of the pathogen-mediated behavior arena is the effect of pathogens on the behavior of uninfected members of the host population and the consequences of such changes on host population dynamics. Our research on the PaV1 virus in spiny lobsters, its inducement of antisocial behavior in uninfected individuals, and the consequences of this pathogen-modulated behavior on lobster population dynamics provides just such an example that we suspect is not novel in the wild.

Summary

This research highlights the need to consider the potential indirect effects of disease in the ecology of infected populations. Resource competition is less common among social organisms; yet, disease alters that paradigm in social spiny lobsters when healthy and diseased lobsters compete, albeit indirectly, for limited shelters. Although diseased lobsters are equally likely to be excluded from shelter when interacting with healthy lobsters, diseased lobsters are more likely to be preyed upon and lobster mortality is generally higher in the open. Higher rates of predation on diseased lobsters along with the aversion that the normally social healthy lobsters display toward diseased conspecifics

together represent natural mechanisms that may limit pathogen transmission through culling and isolation of infected individuals.

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References

- Alzaga V, Vicente J, Villanua D, Acevedo P, Casas F, Gortazar C (2008) Body condition and parasite intensity correlates with escape capacity in Iberian hares (*Lepus granatensis*). *Behav Ecol Sociobiol* 62:769–775
- Behringer DC (2003) The ecological ramifications of density and disease in the Caribbean spiny lobster *Panulirus argus*. Dissertation. Old Dominion University
- Behringer DC, Butler MJ IV (2006) Density-dependent population dynamics in juvenile *Panulirus argus* (Latreille): the impact of artificial density enhancement. *J Exp Mar Biol Ecol* 334:84–95
- Behringer DC, Butler MJ IV, Shields JD (2006) Avoidance of disease in social lobsters. *Nature* 441:421
- Behringer DC, Butler MJ IV, Shields JD (2008) Ecological and physiological effects of PaV1 infection on the Caribbean spiny lobster (*Panulirus argus* Latreille). *J Exp Mar Biol Ecol* 359:23–33
- Behringer DC, Butler MJ IV, Herrnkind WF, Hunt JH, Acosta CA, Sharp WC (2009) Is seagrass an important nursery habitat for the Caribbean spiny lobster, *Panulirus argus*, in Florida? *NZ J Mar Freshw Res* 43:327–337
- Berger DK, Butler MJ IV (2001) Octopuses influence den selection by Caribbean spiny lobster. *Mar Freshw Res* 52:1049–1054
- Bertelsen RD, Butler MJ IV, Herrnkind WF, Hunt JH (2009) Regional characterization of hard-bottom nursery habitat for juvenile Caribbean spiny lobster using rapid assessment techniques. *NZ J Mar Freshw Res* 43:299–312
- Briones-Fourzán P, Lozano-Álvarez E, Negrete-Soto F, Barradas-Ortiz C (2007) Enhancement of juvenile Caribbean spiny lobsters: an evaluation of changes in multiple response variables with the addition of large artificial shelters. *Oecologia* 151:401–416
- Butler MJ, Herrnkind WF (1997) A test of recruitment limitation and the potential for artificial enhancement of spiny lobster (*Panulirus argus*) populations in Florida. *Can J Fish Aquat Sci* 54:452–463
- Butler MJ IV, Lear JA (2009) Habitat-based intraguild predation by Caribbean reef octopus (*Octopus briareus*) on juvenile Caribbean spiny lobster (*Panulirus argus*). *Mar Ecol Prog Ser* 386:115–122
- Butler MJ IV, Stein RA (1985) An analysis of the mechanisms governing species replacements in crayfish. *Oecologia* 66:168–177
- Butler MJ IV, Hunt JH, Herrnkind WF, Matthews T, Childress M, Bertelsen R, Sharp W, Field JM, Marshall H (1995) Cascading disturbances in Florida Bay, USA: cyanobacteria blooms, sponge mortality, and implications for juvenile spiny lobster *Panulirus argus*. *Mar Ecol Prog Ser* 129:119–125
- Butler MJ IV, Herrnkind WF, Hunt JH (1997) Factors affecting the recruitment of juvenile Caribbean spiny lobsters dwelling in macroalgae. *Bull Mar Sci* 61:3–19
- Butler MJ IV, MacDiarmid AB, Booth JD (1999) Ontogenetic changes in social aggregation and its adaptive value for spiny lobsters in New Zealand. *Mar Ecol Prog Ser* 188:179–191
- Butler MJ IV, Behringer DC, Shields JD (2008) Transmission of *Panulirus argus* virus 1 (PaV1) and its effect on the survival of juvenile Caribbean spiny lobster. *Dis Aquat Org* 79:173–182
- Childress MJ (2007) Comparative sociobiology of lobsters. In: Duffy JE, Thiel M (eds) *Evolutionary ecology of social and sexual systems*. Oxford University Press, New York, pp 271–293
- Childress MJ, Herrnkind WF (2001) The guide effect influence on the gregariousness of juvenile Caribbean spiny lobsters. *Anim Behav* 62:465–472
- Dolan TW III, Butler MJ IV (2006) The adaptive value of aggregation among juvenile Caribbean spiny lobster: an evaluation using individual-based modeling. *J Crustac Biol* 26:565–578
- Eggleston DB, Lipcius RN (1992) Shelter selection by spiny lobster under variable predation risk, social conditions, and shelter size. *Ecology* 73:992–1011
- Eggleston DB, Lipcius RN, Miller DL, Coba-Cetina L (1990) Shelter scaling regulates survival of juvenile Caribbean spiny lobster *Panulirus argus*. *Mar Ecol Prog Ser* 62:70–88
- Fero K, Moore PA (2008) Social spacing of crayfish in natural habitats: what role does dominance play? *Behav Ecol Sociobiol* 62:1119–1125
- Forcucci DM, Butler MJ IV, Hunt JH (1994) Growth and population dynamics of juvenile Caribbean spiny lobster, *Panulirus argus*, in Florida Bay, FL (USA). *Bull Mar Sci* 54:805–818
- Foster WA, Treherne JE (1981) Evidence for the dilution effect in the selfish herd from fish predation on a marine insect. *Nature* 293:466–467
- Frank SA (2003) Perspective: repression of competition and the evolution of cooperation. *Evolution* 57:693–705
- Goldstein JS, Matsuda H, Takenouchi T, Butler MJ IV (2008) The complete development of larval Caribbean spiny lobster *Panulirus argus* (Latreille, 1804) in culture. *J Crustac Biol* 28:306–327
- Herrnkind WF (1980) Spiny lobsters: patterns of movement. In: Cobb JS, Phillips BF (eds) *The biology and management of lobsters: physiology and behavior* (Vol. 1). Academic, New York, pp 349–407
- Herrnkind WF, Butler MJ IV (1986) Factors regulating postlarval settlement and juvenile microhabitat use by spiny lobsters, *Panulirus argus*. *Mar Ecol Prog Ser* 34:23–30
- Herrnkind WF, Butler MJ IV, Tankersley RA (1988) The effects of siltation on recruitment of spiny lobsters, *Panulirus argus*. *Fish Bull* 86:331–338
- Herrnkind WF, Butler MJ IV, Hunt JH, Childress M (1997) Role of physical refugia: implications from a mass sponge die-off in a lobster nursery in Florida. *Mar Freshw Res* 48:759–769
- Hixon MA, Beets JP (1993) Predation, prey refuges, and the structure of coral-reef fish assemblages. *Ecol Monogr* 63:77–101
- Holbrook SJ, Schmitt RJ (2002) Competition for shelter space causes density-dependent predation mortality in damselfishes. *Ecology* 83:2855–2868
- Hudson P, Greenman J (1998) Competition mediated by parasites: biological and theoretical progress. *Trends Ecol Evol* 13:387–390
- Hudson PJ, Dobson AP, Newborn D (1992) Do parasites make prey vulnerable to predation? Red grouse and parasites. *J Anim Ecol* 61:681–692
- Hughes WOH, Boomsma JJ (2004) Genetic diversity and disease resistance in leaf-cutting ant societies. *Evolution* 58:1251–1260
- Hughes WOH, Eilenberg J, Boomsma JJ (2002) Tradeoffs in group living: transmission and disease resistance in leaf-cutting ants. *Proc R Soc Lond B* 269:1811–1819

- Ives AR, Murray DL (1997) Can sublethal parasitism destabilize predator-prey population dynamics? A model of snowshoe hares, predators and parasites. *J Anim Ecol* 66:265–278
- Kiesecker JM, Skelly DK (2001) Effects of disease and pond drying on gray tree frog growth, development, and survival. *Ecology* 82:1956–1963
- Koprivnikar J, Forbes MR, Baker RL (2008) Larval amphibian growth and development under varying density: are parasitized individuals poor competitors? *Oecologia* 155:641–649
- Lafferty KD, Morris AK (1996) Altered behavior of parasitized killifish increases susceptibility to predation by bird final hosts. *Ecology* 77:1390–1397
- Lefcort H, Blaustein AR (1995) Disease, predator avoidance, and vulnerability to predation in tadpoles. *Oikos* 74:469–474
- Lefèvre T, Lebarbenchon C, Gauthier-Clerc M, Misse D, Poulin R, Thomas F (2009) The ecological significance of manipulative parasites. *Trends Ecol Evol* 24:41–48
- Lozano-Álvarez E, Briones-Fourzán P, Ramírez-Estévez A, Placencia-Sánchez D, Huchin-Mian JP, Rodríguez-Canul R (2008) Prevalence of *Panulirus argus* Virus 1 (PaV1) and habitation patterns of healthy and diseased Caribbean spiny lobsters in shelter-limited habitats. *Dis Aquat Org* 80:95–104
- Lutermann H, Bennett NC (2008) Strong immune function: a benefit promoting the evolution of sociality? *J Zool* 275:26–32
- Marcogliese DJ, Cone DK (1997) Food webs: a plea for parasites. *Trends Ecol Evol* 12:320–325
- Marx J, Herrnkind WF (1985) Factors regulating microhabitat use by young juvenile spiny lobsters, *Panulirus argus*: food and shelter. *J Crustac Biol* 5:650–657
- Mills DJ, Johnson CR, Gardner C (2008) Bias in lobster tethering experiments conducted for selecting low-predation release sites. *Mar Ecol Prog Ser* 364:1–13
- Mintz JD, Lipcius RN, Eggleston DB, Seebo MS (1994) Survival of juvenile Caribbean spiny lobster: effects of shelter size, geographic location, and conspecific abundance. *Mar Ecol Prog Ser* 112:255–266
- Møller AP, Erritzøe J (2000) Predation against birds with low immunocompetence. *Oecologia* 122:500–504
- Mooring MS, Hart BL (1992) Animal grouping for protection from parasites – selfish herd and encounter-dilution effects. *Behaviour* 123:173–193
- Murray DL (2002) Differential body condition and vulnerability to predation in snowshoe hares. *J Anim Ecol* 71:614–625
- Ostfeld RS, Holt RD (2004) Are predators good for your health? evaluating evidence for top-down regulation of zoonotic disease reservoirs. *Frontiers Ecol Environ* 2:13–20
- Peterson CH, Black R (1994) An experimentalist's challenge: when artifacts of intervention interact with treatments. *Mar Ecol Prog Ser* 111:289–297
- Peterson BJ, Chester CM, Jochem FJ, Fourqurean JW (2007) Potential role of sponge communities in controlling phytoplankton blooms in Florida Bay. *Mar Ecol Prog Ser* 328:93–103
- Poulin R, Fitzgerald GJ (1989) Shoaling as an anti-ectoparasite mechanisms in juvenile sticklebacks (*Gasterosteus spp*). *Behav Ecol Sociobiol* 24:251–255
- Pulliam HR (1973) On the advantages of flocking. *J Theo Biol* 38:419–422
- Ratchford SG, Eggleston DB (1998) Size- and scale-dependent chemical attraction contribute to an ontogenetic shift in sociality. *Anim Behav* 56:1027–1034
- Reinhard EG (1950) An analysis of the effects of a sacculinid parasite on the external morphology of *Callinectes sapidus* Rathbun. *Biol Bull* 98:277–288
- Schaffer MW, Jensen DB, Hobbs DE, Gurevitch J, Todd JR, Schaffer MV (1979) Competition, foraging energetics, and the cost of sociality in 3 species of bees. *Ecology* 60:976–987
- Schmidt KA, Ostfeld RS (2001) Biodiversity and the dilution effect in disease ecology. *Ecology* 82:609–619
- Shields JD, Behringer DC (2004) A new pathogenic virus in the Caribbean spiny lobster *Panulirus argus* from the Florida Keys. *Dis Aquat Org* 59:109–118
- Smith KN, Herrnkind WF (1992) Predation on early juvenile spiny lobsters *Panulirus argus* (Latreille): influence of size and shelter. *J Exp Mar Biol Ecol* 157:3–18
- Söderbäck B (1994) Interactions among juveniles of two freshwater crayfish species and a predatory fish. *Oecologia* 100:229–235
- Sousa WP (1991) Can models of soft-sediment community structure be complete without parasites? *Am Zool* 31:821–830
- Steele MA (1999) Effects of shelter and predators on reef fishes. *J Exp Mar Biol Ecol* 233:65–79
- Stevely JM, Sweat DE (1998) Survey of recovery of Florida Keys sponge populations following a widespread sponge mortality. Report No. MR252, Florida Sea Grant Extension Program. Tallahassee, Florida.
- Temple SA (1987) Do predators always capture substandard individuals disproportionately from prey populations? *Ecology* 68:669–674
- Thompson RM, Mouritsen KN, Poulin R (2005) Importance of parasites and their life cycle characteristics in determining the structure of a large marine food web. *J Anim Ecol* 74:77–85
- Vorburger C, Ribi G (1999) Aggression and competition for shelter between a native and an introduced crayfish in Europe. *Freshw Biol* 42:111–119
- Weiss HM, Lozano-Álvarez E, Briones-Fourzán P (2008) Circadian shelter occupancy patterns and predator-prey interactions of juvenile Caribbean spiny lobsters in a reef lagoon. *Mar Biol* 153:953–963