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Temporal shift in the presence of a chemical cue contributes to a diel shift in sociality

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Spatial and temporal variation in animal aggregations may be due to variation in the presence of cues for aggregation (or disaggregation) or to variation in the receptivity of the animal to a particular cue or suite of cues. Spiny lobsters, *Panulirus argus*, forage solitarily but are often found aggregated in their diurnal shelters. An important proximate cause of aggregation among spiny lobsters is a scent they produce that influences shelter choice by conspecifics. We examined how variability in the presence of, or response to, such a chemical cue may contribute to diel shifts in sociality among spiny lobsters. We conducted a series of Y-maze shelter choice experiments using lobsters that were either maintained under altered dark:light schedules in the experimental arena or under natural lighting in the head tanks. Lobsters that were maintained on a light schedule 8 h later than normal chose shelters at their dawn (corresponding to the middle of the night for lobsters in the head tanks); however, their choices of shelter were not influenced by scents of conspecifics. Lobsters that were maintained on a schedule 8 h earlier than normal chose shelters in the middle of their night (corresponding to dawn for the lobsters in the head tanks). Their choices of shelter were significantly influenced by conspecific scents. These results suggest that the chemical cues for aggregation, released by spiny lobsters, are present discontinuously, that spiny lobsters are influenced by conspecific odours continuously, and that aggregation is controlled by temporal variation in the presence of a chemical cue.

The formation of groups often leads to dramatic variation in distribution and abundance patterns of mobile animals. Herds of African plains mammals, flocks of birds and schools of fish are highly visible examples of patchy distributions resulting from social behaviour. Thus, temporal variation in group formation may lead to significant changes in distribution and abundance patterns of animals. In terrestrial systems, seasonal shifts in sociality are noted among many species of birds that are territorial during summer but migrate and feed in flocks at other times of the year (Pulliam & Caraco 1984), as well as among baboons, whose group size changes during the course of the day (Kummer 1968). Temporal variation in group formation is common among many aquatic organisms. Examples of seasonal spawning aggregations can be found in such diverse species as Nassau grouper, *Epinephelus striatus* (Colin 1992), red king crabs, *Paralithodes camtschatica* (Stone et al. 1993) and epitokous palolo worms, *Eunice viridis* (Caspers 1984). Larval dispersion and subsequent gregarious recruitment are common among sessile invertebrates (reviews by Burke 1986; Pawlik 1992) and reef fish (Sweatman 1988). Many pelagic fish disperse at dusk and aggregate at dawn in schools, while zooplankton form temporary aggregations following nocturnal migrations to surface waters (review by Mangel & Clark 1988).

Spatial and temporal variation in animal aggregations may be due to variation in the presence of cues for aggregation (or disaggregation) or to variation in the receptivity of the animal to a particular cue or suite of cues. Flocks of cliff swallows flying to patches of insects form when unsuccessful foragers follow successful foragers to patches (Brown 1986). Birds watch nearby nests for cues of successful foraging, such as feeding of nestlings, and leave their nests to follow these foragers if they were unsuccessful on their last excursion (Brown 1986). Birds that were successful leave independently of other successful birds (Brown 1986). Fish schools form using visual cues of neighbouring fish and in response to the level of predation risk (Magurran & Seghers 1991; Ryer &

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Olla 1991). Some fish do not form schools at night (Freon et al. 1995), presumably due to the lack of visual cues.

The spiny lobster, *Panulirus argus*, is an interesting model for studying group formation because it shows ontogenetic, diel and spatial variation in forming groups at its daytime shelter. After a protracted larval, planktonic stage of 6–9 months, postlarvae settle in nearshore nursery grounds and reside almost exclusively solitarily for 3–4 months in clumps of macroalgae or other structurally complex habitats (Andree 1981; Marx & Herrnkind 1985a, b). After this 'algal phase', early juvenile *P. argus* shift to diurnal sheltering in crevices and under sponges and branching octocorals (Forcucci et al. 1994). During the postalgal phase through adulthood, spiny lobsters can often, but not always, be found sharing their diurnal shelters (Herrnkind et al. 1975; Eggleston & Lipcius 1992), although they forage solitarily at night.

An important proximate cause of aggregation in this species is a scent produced by lobsters that affects the shelter choice of conspecifics. Scents emanating from postalgal phase juvenile (Ratchford & Eggleston 1998) and adult lobsters (Ratchford & Eggleston 1998; R. K. Zimmer-Faust & N. D. Pentcheff, unpublished data) positively influence shelter selection by conspecifics; *P. argus* will choose an occupied shelter over an unoccupied shelter, leading to aggregation. Adults of other species of spiny lobsters, *P. interruptus* (Zimmer-Faust et al. 1985) and *Jasus edwardsii* (M. Butler, unpublished data), also produce and release odours that influence shelter choice. By 'release' we do not wish to imply any control over the flow of the chemical cue from the lobster, merely that production of the odour may be temporally separated from its emanation from the lobster. In contrast, although it is not known whether algal phase lobsters produce such a scent, shelter choice among algal phase *P. argus* is not influenced by conspecific scents (Ratchford & Eggleston 1998). The variation in the presence of and receptivity to lobster odours may explain the shift in sociality from solitary to gregarious shelter usage in algal phase and postalgal phase lobsters, respectively (Ratchford & Eggleston 1998). In this study, we examined how variability in the presence of or response to an odour may contribute to diel shifts in sociality among spiny lobsters.

The tendency for spiny lobsters to aggregate varies during the course of the night (Zimmer-Faust et al. 1985). For example, spiny lobsters usually forage solitarily at night but may be found sharing shelters by dawn. During overnight shelter choice experiments (Ratchford & Eggleston 1998), lobsters did not reside in shelters at night, although they explored the shelters provided. The first shelter they visited was not necessarily the one they chose by the following morning, nor did they first explore the shelter from which the odour of conspecifics emanated, although in most cases they eventually chose to reside in this shelter by dawn. Such observations stimulated the question of how diel changes in aggregation among spiny lobsters are regulated. If aggregation among lobsters is controlled by temporally regulated receptivity, then chemical cues may emanate from lobsters all day, but lobsters are receptive to these cues only near dawn (when they are seeking shelter), or perhaps with increasing light. If aggregation is controlled by the temporally regulated presence of chemical cues, then these chemical cues may emanate from lobsters only near dawn or with increasing light, but lobsters are receptive to these conspecific cues at any time of day.

METHODS

We captured 90 lobsters from shallow reefs near Lee Stocking Island, Bahamas, with tail snares or large aquarium nets. We measured the carapace length of each lobster and tagged each at the base of its antennae with a unique sequence of coloured plastic cable ties to aid in the identification of individuals. We held the lobsters in an outdoor, shaded wet-laboratory at the Caribbean Marine Research Center on Lee Stocking Island in a tank (2.4 × 1.2 m and 0.3 m deep) containing concrete block shelters for up to 3 weeks prior to use. We allowed the lobsters to acclimate for 3 days prior to use in any experiment. We fed the lobsters daily between 1600 and 1800 hours a diet of live snails, *Cerithium* spp., and chopped conch, *Strombus gigas*. Temperature in the holding tanks was 22–27°C. All lobsters were released after use.

Y-maze Shelter Choice Experiments

We conducted a series of shelter choice experiments in February and March 1998 in a Y-maze (described in Ratchford & Eggleston 1998) in an outdoor, shaded wet-laboratory. Lobsters were given a choice of two shelters that differed only in that one shelter received water that had flowed through a head tank containing conspecifics while the other shelter received water that had flowed through an empty head tank (Fig. 1). Test lobsters, which would be allowed to choose a shelter in the experimental arena, were subjected to altered dark:light cycles for a week to shift the timing of their shelter-seeking and foraging behaviour. The altered dark:light schedule was continued during the Y-maze experiments by using a curtain to enclose the experimental arena (but not the head tanks), as well as artificial lighting over this arena, but not over the head tanks.

From previous experiments (Ratchford & Eggleston 1998) we know that the chemical cue that influences shelter choice must be present near dawn and that lobsters are receptive to this cue near dawn, as lobsters chose shelters from which conspecific odours flowed near dawn. To determine whether lobsters are continuously receptive to cues from conspecifics, we conducted shelter choice experiments to test specifically whether lobsters are receptive to the chemical cues at one critical period, in the middle of night, when lobsters would normally be foraging solitarily. Because the odour is present at dawn, we conducted a shelter choice experiment at dawn using lobsters maintained under natural light conditions in the head tanks. To ensure that the lobsters in the experimental arena would behave as if it were the middle of their night, we adjusted the dark:light schedule 8 h earlier than the natural schedule by maintaining the lobsters under

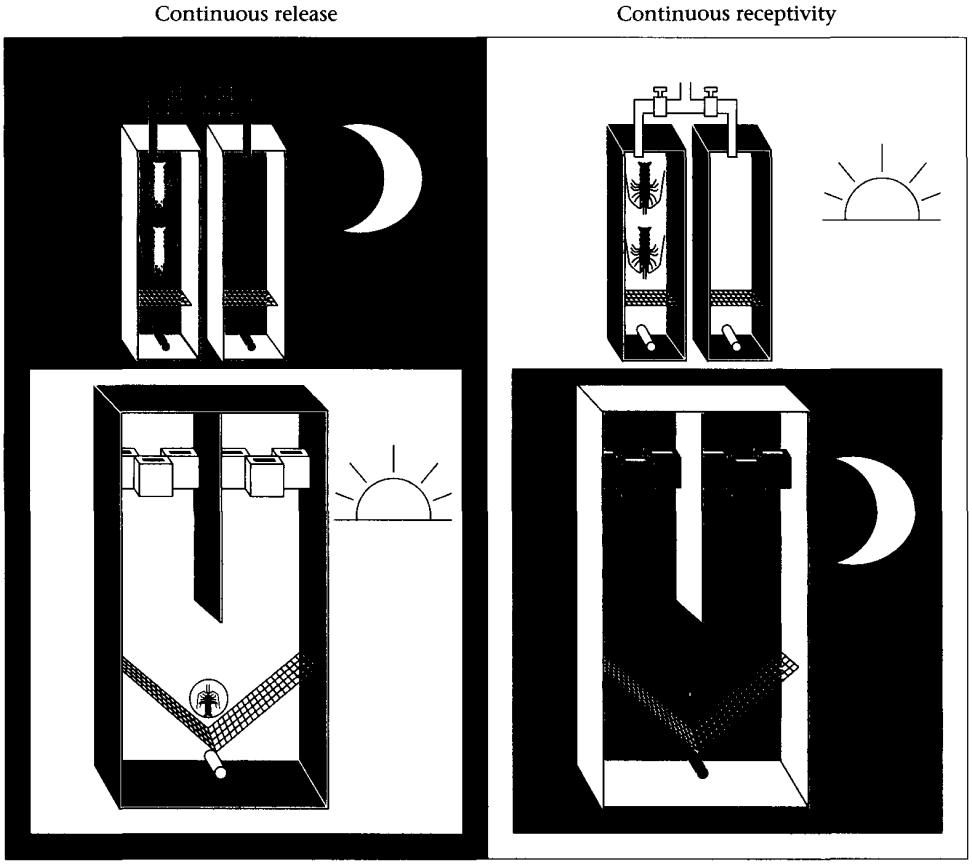

Figure 1. Schematic of Y-maze experimental arenas. Unfiltered sea water flowed through two head tanks, one of which contained two conspecifics, then into the arms of the Y-maze containing concrete shelters, and out through a standpipe behind the start area. A single experimental lobster was placed at the start area of the maze and allowed to choose a shelter over a 4 h period. The head tanks were exposed to natural light conditions. The experimental arena was enclosed in an opaque tent and subjected to shifted dark:light conditions.

an artificial 12:12 h dark:light cycle (see Altering Diel Behaviour below). We randomly selected two lobsters (carapace length: 49–82 mm) maintained under natural lighting conditions and placed them within a randomly chosen head tank just prior to dawn (0400 hours). We placed a lobster raised on the '8 h earlier' (8HE) artificial light schedule for 7 days in a wire cylinder acclimating ring at the start area of the Y-maze arena (Fig. 1), and allowed it to acclimate for 15 min in the dark before removing the ring. The experiment ran for 4 h, until approximately 2 h after sunrise. The experimental lobster remained in the dark throughout the trial (as this would be 2000 to 0000 hours for the lobster in the experimental arena that was raised on the artificial light cycle). If the experimental lobsters chose shelters receiving water from the head tank containing the conspecifics, this experiment would demonstrate that lobsters are receptive to conspecific odours even at night when lobsters have usually dispersed, and would suggest that aggregation among lobsters noted at dawn is not regulated by changes in receptivity to attracting odours but, instead, is regulated by changes in the presence of attracting odours.

To determine whether lobsters release chemical cues continuously, we conducted shelter choice experiments to test specifically whether lobsters release the odours in the middle of the night. Lobsters that were used in the head tanks were maintained under natural light conditions. The light:dark schedule of the lobsters to be used in the experimental arena had to be adjusted 8 h later (8HL) than the natural schedule so that the lobsters would behave as if it were dawn, because lobsters should make a shelter choice near dawn and are influenced by odours at dawn. We placed two lobsters (carapace length: 45–84 mm) maintained under natural lighting conditions in a randomly chosen head tank at 2000 hours. We placed a lobster maintained for 7 days on an altered 8HL light schedule in a wire cylinder acclimating ring at the start area of the Y-maze arena (Fig. 1), and allowed it to acclimate for 15 min in the dark before removing the ring. After 2 h, we turned on the light over the arena (i.e. simulating dawn for the lobster in the experimental arena raised on the artificial 8HL light cycle). The experiment continued for an additional 2 h. If the maze lobsters chose shelters receiving water from the head tank containing the conspecifics, this experiment would demonstrate that conspecific odours are produced even at night when lobsters have usually dispersed, and would suggest that aggregation among lobsters noted at

dawn is regulated by changes in receptivity to conspecific odours.

No lobster was used more than once in the head tanks during each experiment, and no lobster was used in the experimental arena more than once. We analysed the results of the two shelter choice experiments as separate one-tailed binomial tests (Zar 1984) where, as a null hypothesis, the probability of choosing the shelter receiving water from the tank containing the conspecific was 0.5. We chose a one-tailed test because we were testing only whether aggregation by lobsters was positively influenced by the odour of conspecifics.

Altering Diel Behaviour

In an attempt to alter the timing of the lobsters' activity and sheltering, we maintained several large lobsters for 7–10 days under artificial (12:12 h dark:light) light cycles that were 8 h off their normal schedule, before using them in the Y-maze shelter choice experiments described above. Lobsters (carapace length: 45–84 mm) were held in one of three rooms containing 180 litre tanks with continuous flowing sea water. Two lobsters were placed in each tank. Each tank contained a concrete block shelter at one end. One 60-W incandescent bulb on a timer with 12:12 h dark:light cycle was positioned in the centre of the ceiling of each room. The light in the room in which lobsters were kept under the normal light cycle (NORM) was turned on from 0600 to 1800 hours. The lights in the other rooms were turned on from 1400 to 0200 hours or from 2200 to 1000 hours for lobsters maintained on schedules 8 h later (8HL) than the normal schedule or 8 h earlier (8HE), respectively. Food (e.g. conch meat) was placed in the holding tanks at the start of the dark cycle.

We conducted behavioural observations to search for evidence that the activity patterns of lobsters raised under altered light cycles had been shifted. Specifically, every 4 h for 7 days, we quantified behaviours characteristic of nocturnal activity, such as foraging and walking (Lipcius & Herrnkind 1982), and diurnal sheltering behaviour. A lobster was considered to act in a Phase Correct manner if it was either clearly active (walking, climbing, or in a position away from a shelter) during its dark cycle, or in its shelter during its light period. Similarly, Phase Incorrect responses included remaining in the shelter during the dark cycle as well as showing activity during the light cycle. During any observation period, lobsters that were inactive but located on, in front or to the side of, or behind the shelter could not be scored as displaying Phase Correct or Phase Incorrect behaviours.

We predicted that lobsters under the altered light cycles would initially display more Phase Incorrect behaviours than the lobsters under the normal light schedule, and that over time, the percentage of Phase Incorrect behaviours displayed by the lobsters under the altered light cycles would be similar to those of the lobsters on the normal light cycle. To test this prediction, we compared the proportion of Phase Incorrect responses by day of 12 lobsters in the 8HE treatment, 12 lobsters in the 8HL treatment and four lobsters on a NORM cycle with a repeated measures ANOVA with time (day) as the repeated measure. The response variable (proportion of Phase Incorrect responses) was arcsine square-root transformed to ensure homogeneous variances and normality.

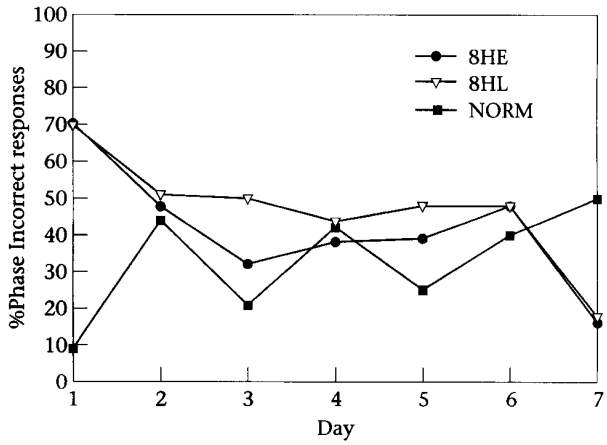

Figure 2. The percentage of Phase Incorrect behaviours noted among lobsters on normal light cycles (NORM) and light cycles shifted 8 h earlier (8HE) and 8 h later (8HL) over 7 days. A behaviour was scored as Phase Incorrect if the lobster was active during the light part of its cycle (when it would normally reside within a shelter), or was occupying a shelter during the dark portion of its cycle (when it would normally be actively foraging away from its shelter). Responses by lobsters undergoing altered light cycles were different from NORM lobsters only on the first day of the study (see text for significance levels).

RESULTS

Altering Diel Behaviour

Lobsters that were subjected to altered dark:light cycles often occupied the concrete shelters during the light period, usually ate all the food within one observation period, and despite the limited space in holding tanks, were active, as evidenced by their walking around the tank and climbing on the shelter. Nevertheless, the lobsters were often found motionless on or beside the concrete shelter, leading to behaviours being scored on only 50–65% of occasions within the three treatments.

The behaviour of lobsters varied according to their dark:light schedule treatment and by time; there was a significant day × treatment interaction effect ($F_{6,5}=15.05$, $P=0.005$). On day 1, lobsters subjected to the altered dark:light cycle displayed Phase Incorrect behaviours on 75% of occasions (Fig. 2). Lobsters on a normal dark:light cycle displayed Phase Incorrect responses only 10% of the time on the first day, and acted in a Phase Incorrect manner on an average of 29% of occasions throughout the observation period (Fig. 2). The proportion of behaviours scored as Phase Incorrect among lobsters with altered dark:light cycles decreased from approximately 75 to 50% from day 1 to day 2, then fluctuated relatively little over the remainder of the experiment (Fig. 2). The proportion of Phase Incorrect responses among lobsters

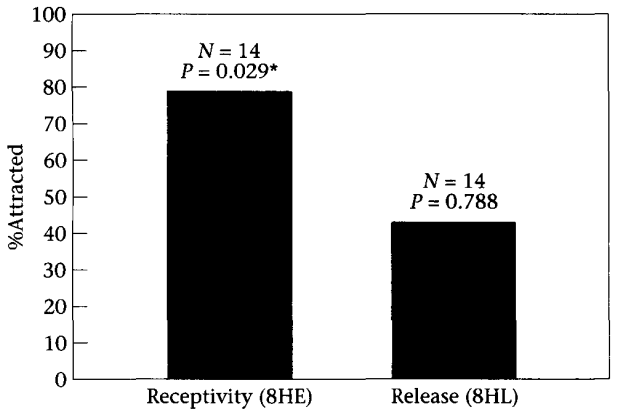

Figure 3. Results of two Y-maze experiments testing whether lobsters continuously release odours that are attractive to conspecifics or are continuously receptive to odours of conspecifics. Shelter choice by lobsters acclimated to a light cycle shifted 8 h earlier (8HE) than their normal light cycle was significantly influenced by conspecifics, whereas shelter choice by lobsters acclimated to a light cycle shifted 8 h later (8HL) was not. *P* values were based on a one-tailed binomial test (Zar 1984), where the probability of choosing a shelter having the conspecific odour was 0.5.

undergoing the altered dark:light cycle was lowest on day 7; however, no significant difference in the proportion of Phase Incorrect behaviour was detected after the first day ($P>0.300$). Although there were no differences in the proportion of Phase Incorrect behaviours between the three treatments (8HE, 8HL and NORM) by the second day of light cycle shift, we chose a conservative approach and used lobsters conditioned for at least 7 days on altered light cycles in subsequent Y-maze shelter choice experiments.

Y-maze Shelter Choice Experiments

In experiments conducted from 2000 to 0000 hours, lobsters maintained on the 8HL schedule were usually found residing in shelters at the end of the experiment, which corresponded to just after dawn on their altered cycle. One of the 16 lobsters made no choice, remaining at the start area of the arena; this trial was disregarded. One other trial was disregarded due to the collapse of the curtain into the arena overnight. Of the other 14 trials, only six lobsters chose the shelter receiving water from the head tank containing the conspecifics ($P=0.788$; Fig. 3). During the middle of the night, the lobsters in the head tanks did not influence the shelter choice of the lobsters in the Y-maze. Thus, lobsters do not appear to release the cue continuously.

In experiments conducted from 0400 to 0800 hours, lobsters maintained on the 8HE schedule were also usually found residing in shelters at the end of the experiment, although this time corresponded to midnight on their altered cycle. Three of the 14 lobsters were moving at the end of the trials. One lobster moved out of and then back into the shelter receiving water from the conspecific shelter; this lobster was scored as choosing the conspecific shelter. Two other lobsters switched shelters repeatedly. These lobsters were scored as not choosing the conspecific shelter. All other lobsters were stationary and residing in a shelter. Overall, 11 of 14 lobsters ($P=0.029$) chose the shelter receiving water from the head tank containing the conspecifics (Fig. 3). At dawn, the presence of lobsters in the head tanks significantly influenced the behaviour of the lobsters in the Y-maze, even though the lobsters in the Y-maze would normally be foraging solitarily on this schedule. Thus, lobsters appear to be receptive to conspecific odours continuously, rather than only at dawn when they aggregate at their shelters.

DISCUSSION

Spiny lobsters are active at night; they leave their shelters at dusk to forage, and return to shelters at or before dawn (Kanciruk & Herrnkind 1973; Herrnkind et al. 1975). We were able to shift the activity schedules of spiny lobsters in the laboratory under varying dark:light cycle regimes in just a few days. Significant differences in activity were noted only on the first day between lobsters on the altered light cycle and those on a normal cycle. Fielder (1965) reported that *Jasus novahollalandei*, placed on reciprocal dark:light cycles, were active during the daytime when maintained in the dark and were inactive during night when maintained under light, even on the first day of their study. Apparently, the level of light significantly affects the activity patterns of *P. argus* and other spiny lobsters. For example, strong moonlight inhibits *P. argus* activity (Sutcliffe 1956). We have noted on several occasions that lobsters will leave their shelters earlier on cloudy days than on clear days. Even fairly weak light levels will reduce the activity of Japanese spiny lobsters, *Panulirus japonicus* (Nagata & Koike 1997).

The shelter choices of several species of spiny lobsters, including *P. interruptus* (Zimmer-Faust et al. 1985), *P. argus* (Ratchford & Eggleston 1998) and *J. edwardsii* (M. Butler, unpublished data), are affected by odours emanating from conspecifics. At least among *P. argus*, this odour is not released all night; rather, it is released only during early morning hours when lobsters are returning to shelters following their solitary, nightly foraging excursions. In the experiment that tested temporal shifts in release of the odour, the 8HL lobsters chose a shelter by the end of the experiment, corresponding to a time after their dawn, but showed no preference for the shelter receiving water from the head tank containing the conspecifics. It was midnight for lobsters in the head tank. If lobsters in the head tanks released a chemical cue all night, the lobsters in the maze should have shown a preference for shelters from which the scent was emanating. Conversely, in the experiment that tested temporal shifts in receptivity to the odour, most lobsters in the Y-maze chose a shelter by the end of the experiment, even though this corresponded to the middle of their night, and preferred the shelter receiving water from the tank containing the conspecifics. It was dawn for lobsters in the head tank.

Thus, we conclude that the lobsters in the head tank released a chemical cue near dawn but not around midnight, and therefore, that spiny lobster aggregation appears to be regulated by temporal changes in the presence of an odour rather than temporal shifts in receptivity to the odour.

Lobsters in the experimental arena were conditioned under altered light regimes for several days prior to their use in shelter choice experiments. The opaque tent and artificial lighting in the arena allowed continuation of the altered light regimes throughout the duration of the shelter choice experiments. The transitions from dark to light and from light to dark were not gradual as they are in the wild, but an abrupt turning on or off by a switch. We could not make observations in the experimental arena when lights were off as light might have entered the arena, influencing the lobsters; however, we were able to observe the lobster in the arena in the experiment in which the light was turned on to mimic dawn. No lobster made a choice within 10 min of the lights turning on; all were either already sheltered or made shelter choices over the next 2 h. These observations suggest that lobsters were not panicked into making a shelter choice by the abrupt change in light conditions.

Almost all lobsters chose a shelter by the end of the trial whether the end corresponded to their dawn or their midnight. We had expected lobsters to seek shelter at their dawn, given the shift in activity patterns during conditioning; they did. All but one lobster chose a shelter at their simulated dawn. This result was pleasantly surprising given that none of the lobsters had acted in a Phase Correct manner at all observed occasions during the acclimation period to alter their diel behaviour. We were also surprised that lobsters chose a shelter at their simulated midnight because this behaviour is inconsistent with our expectations that lobsters would be active at this time and inconsistent with the active behaviour often displayed during the dark periods of acclimation to the altered light schedule. The presence of a specific odour or set of odours emanating from conspecifics may be a cue to begin shelter search or choice.

Although our findings support the conclusion that diel shifts in aggregation among spiny lobsters are controlled by temporal variation in the release of an attracting odour, this does not necessarily imply that the lobster releasing the odour controls its release or stands to benefit from the odour. We know nothing about the chemical composition of the odour, and little about its point of origin. The odour may be a metabolic product that is passively released primarily at certain times, such as near dawn, or it may be a specific pheromone. The odour may not be a single compound, but a mix such that each component appears in appropriate concentrations only at a certain time. The nature of aggregation among spiny lobsters generated by this odour may range from completely benefiting the releaser to completely benefiting the receiver; however in the case of *P. argus*, there is sufficient evidence to suggest that there are benefits to the releasing and receiving lobsters. For example, survival of large lobsters increases with group size (Mintz et al. 1994; M. Butler, unpublished data), although small lobsters show no increase in survival when residing in groups with other small lobsters, as opposed to residing solitarily (Childress 1995; M. Butler, unpublished data). Several authors have suggested that the barrier presented by several sets of waving large spinose antennae may prevent predators from penetrating a shelter housing a group of lobsters (Berrill 1975; Cobb 1981; Zimmer-Faust & Spanier 1987). Large, subadult and adult lobsters may be better able to defend themselves in groups using their stiff antennae than smaller lobsters. Small spiny lobsters may benefit from locating shelters containing larger lobsters that can defend the shelter. Shelter sharing among small, juvenile spiny lobsters has been proposed to be the result of a 'guide effect', whereby lobsters use cues from other lobsters to find shelter more quickly (Childress 1995; Childress & Herrnkind 1997). Lobsters may not only use conspecific cues to locate a shelter, but also to judge the quality of the shelter (unpublished data).

Several questions remain unanswered. Do lobsters release the cue only when they have located a shelter, or do returning lobsters also release the cue? If returning lobsters release the cue, how could they distinguish their own odour from those of conspecifics? If lobsters can distinguish individual odours, can they then assess the number of conspecifics in an area? When do lobsters discontinue release of the cue? As we answer some of these questions, we will more completely understand how aggregations of lobsters form.

Group formation is an important behaviour among social animals. Behavioural ecologists have emphasized the study of why animals form groups, but little is known about how animals form groups. In this study, proximate causes of animal aggregation were elucidated through the study of variation in the presence of cues for aggregation and variation in receptivity to cues. Such a framework for the study of animal aggregation may be useful in studying the formation of nonkin groups such as flocks of birds, schools of fish and swarms of insects. We recently demonstrated that the ontogenetic shift in sociality among spiny lobsters is due to temporal shifts in both receptivity to olfactory cues for aggregation and a mass-dependent release of such cues (Ratchford & Eggleston 1998). In this study, we showed that the diel shift in spiny lobster aggregation at diurnal dens depends upon a temporal shift in the presence of a scent released by conspecifics.

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