



Self-ordering in the distribution of limpets: The role of previous occupants



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ABSTRACT

One of the most important determinants of fitness is the location of an animal within its habitat, and it is assumed that habitat patches are differentiated by the resource value to an organism. For many invertebrates, we have no idea which resource axes may be important, and moreover, we do not necessarily understand the value of micro-habitat. For non-homing animals, the distribution of animals is often thought to be indicative of food or refuge resources. Using manipulative experiments, we show that the distribution of the limpet *Cellana tramoserica* is dependent on the previous occupants of any particular resting site. If limpets are removed, incoming limpets will occupy previous resting sites in a much greater proportion than occupying new resting sites, noting that *C. tramoserica* is not an obligate homing species. It was likely that a chemical-based cue bound to the substratum surface is a strong modifier for whether limpets re-occupied sites. There was some evidence that this pattern held also for animal sizes, such that the size of original occupant predicted that of the incomer. These experiments provide new evidence that decisions to occupy a resting site may not solely be based on resource values but also are associated with public information about site suitability.

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1. Introduction

Understanding the ecological effects of animal behaviours and interactions requires us to know where animals are and, preferably, the underlying reasons for the observed distribution (Andrewartha and Birch, 1954). It could be argued that quantifying and predicting the distribution of animals are the cornerstones of understanding the ecology of animals. Given the context of changes in distribution and/or ranges associated with climate change, the need for knowledge of the causal basis for patterns of animal distribution is critical (Berggren et al., 2009). At its most basic, understanding the distribution of animals in space requires us to quantify habitat properties and link these to population processes (Andrewartha and Birch, 1954; Berggren et al., 2009). This problem has particular importance when the biota concerned may have strong ecosystem level effects.

Many grazing invertebrates are sedentary, so their habitats simultaneously represent a foraging arena and also a place to rest/hide during non-foraging phases. Consequently, understanding the distribution of animals in this context means simultaneously quantifying the properties of the foraging arena and those of the sites used as refugia. For many organisms, we have a good understanding of how habitat properties affect feeding locations (Simpson et al., 2010), and this is

particularly true of invertebrate herbivores (Lewinsohn et al., 2005). This capacity to explain spatial distribution of consumers in respect of their foodscape (Gordon, 2008) is not matched by our ability to explain the choice of where animals rest during non-foraging/unfavourable periods. This lack of understanding is scale-dependent. For example, we know that certain habitat properties (relative humidity; Cook, 1981; temperature; Pincebourde et al., 2007; topography; Fraser et al., 2014) may modify the spatial arrangement of some animals; in contrast though, we also know that desiccation risk *per se* is not changed by limpets having different small-scale distributions (Coleman, 2010). There is, however, much less knowledge on how a given habitat property may influence an individual to use a given resting site within that habitat. We can observe snails resting in certain locations (Miller et al., 2009) or moths on specific individual trees of a given species (Kang et al., 2013), but we have little idea as to the reason why that given piece of rock or the location on that piece of bark was chosen by that individual animal. This means that an underlying explanation for the oft-stated highly variable patterns of spatial dispersion of animals is lacking. The model system we chose to illustrate this problem is the distribution of limpets on the rocky shore. Aside from any problems of homing (Branch, 1981; Coleman, 2007; Frank, 1964), it could be assumed that all rock surfaces within the tidal range of the animal would be suitable habitat. Consequently, the reasons for consistent non-random patterns of distribution (Coleman, 2010) could be that the habitat is not uniform, and specific locations are utilised more frequently than others.

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The limpet *Cellana tramoserica* Holten 1802 is an abundant grazer on rocky shores of south-eastern Australia (Edgar, 2000). It grazes the surface of rocky substrata removing biofilms and algal propagules (Murphy and Underwood, 2006). In common with many other limpet species, it exerts an extremely strong habitat structuring effect, controlling habitat state and variability (Branch, 1985; Coleman et al., 2006; Southward, 1964). One of the notable features of limpets on rocky shores is a strong pattern of non-random distributions (Coleman et al., 1999; Coleman et al., 2004b; Fraser et al., 2014). In common with other invertebrates, such non-random distributions are often explained in the context of reduction of risk from predators (Coleman et al., 2004a) and/or abiotic stressors (see Coleman, 2010 for review). The possibility that habitat properties and infochemical-based interactions may contribute to these observed patterns has not yet been tested. Many invertebrates receive information about their habitats using modalities such as vibration (e.g. from predation; Coleman et al., 2004a) or infochemicals via dissolved or surface-bound cues (Hay, 2009). In addition to containing cues about identity (Funke, 1968; Shaheen et al., 2005), which are important for predator–prey relationships or social networks, surface-bound chemical cues such as mucous trails laid by molluscs or stationary mucus to facilitate attachment can contain information on many other aspects of the emitting organism's biology (Davies and Hawkins, 1998; Ng et al., 2013). For molluscs such as limpets, perception of their chemical environment occurs through chemosensory apparatus on their external membranes (Croll, 1983) and via ingestion of biofilms/mucus (Davies and Hawkins, 1998), which themselves contain chemical cues (Croll, 1983).

In many limpet species, patterns of distribution are explained by 'homing'; in fact, limpets are often used as classic examples to illustrate this behaviour (Coleman, 2007). Homing is described as when individuals return to the same place and are repeatedly observed over a given period of time (Frank, 1964; Mackay and Underwood, 1977). This does not, however, explain how patterns of distribution are established or maintained irrespective of individual identity. If an individual is removed, and its space is reoccupied by different individuals, then the overall pattern of distribution is maintained, and unless identity is controlled for, this result would be treated as 'homing'. One mechanism that could lead to limpets re-occupying previously used sites is the existence of mucus secreted by the previous individuals (Davies and Hawkins, 1998; Grenon and Walker, 1981). During the non-foraging phase, limpets secrete stationary mucus to facilitate attachment (Grenon and Walker, 1981) and enable clamping behaviours (Smith, 2002). This stationary mucus is chemically different from pedal mucus (Smith et al., 1999), and unlike pedal mucus, this stationary mucus is not re-ingested on departure, so due to its insolubility in water (Smith et al., 1999), it remains in place unless grazed by other individuals. We term these remnant mucus patches 'mucus pads' to distinguish them from mucous trails left by foraging gastropods. If a mucus pad is left unoccupied, a subsequent occupant of that site could save energy by using it as a resting site as this incoming limpet would need to secrete less stationary mucus for attachment, than if it had to create a mucus pad from scratch; this requires a close match in size between the limpet that made the mucus pad and the incoming one, as the margin of the foot has to be in contact with mucus pad (Grenon and Walker, 1981; Smith, 2002). An important problem that needs solving to understand the role of mucus pads in the spatial arrangement of limpets is that researchers need to remove mucus without disturbing any other habitat property. Instead of using acid/bleach (low viscosity and may flow off the test site to affect nearby biota) or wire brushing (confounds mucus removal by simultaneously altering the physical surface of the substratum), one possibility is to use paint stripper. This is very viscous and dries to a powder, so does not influence the rest of the assemblage.

If the location of limpets were maintained, over shorter timescales, by the re-occupation of limpet resting sites, we would predict that in the event of a resting site being vacated, incoming limpets would be

more likely to occupy previously utilised resting sites than other pieces of rock. Moreover, owing to the need to fit to a mucus pad, it would be expected that 'new' limpets would either be the same size or be slightly smaller than the original occupant. Providing there are no artefacts of the removal process, we further predicted that removal of the limpet mucus pads would result in disruption of patterns of re-occupancy.

2. Methods

2.1. Pilot. If limpet resting sites become available, where do new/incoming limpets go?

The prediction that previously occupied places would be more likely to be re-occupied than places not previously occupied was tested by a simple removal experiment. Since *C. tramoserica* does not home consistently (Mackay and Underwood, 1977), we refer to the location of a limpet as a resting site rather than a 'home-scar' (Coleman et al., 2004b). In a pilot experiment (May 2009) in each of two patches at Cape Banks Special Scientific Reserve (hereafter 'Cape Banks'; 34° 59' S, 151° 25' E), we either removed all of the limpets in a 50 × 50 cm plot ($n = 8$) using a palette knife slid under the foot or left them *in situ*. Removed limpets were displaced (up to 30 cm away) so that local densities were not disrupted, and re-attached by placing onto a wet surface (Underwood, 1978). This displacement also meant that the moved limpets could not follow a trail back to their resting site. Plots were a minimum distance of 2 m apart. Each plot was marked with a numbered tag attached with a screw in the rock with an additional hole drilled into the rock to provide orientation of the subsequent photographic image. Prior to manipulation, each plot was photographed and the limpets removed, or not, according to a random allocation of treatment. After three days, which is sufficient for all limpets present to leave their resting sites to forage (R.A. Coleman, unpubl. observ.), each plot was re-photographed. The photographs were examined side-by-side by a person blind to the original treatments and not involved in the fieldwork. By comparing the location of limpets in the time 2 photograph (hereafter 'new limpets') with the location of limpets in resting sites at time 1, it was possible to calculate what proportion of resting sites in the time 1 image were re-occupied by new limpets. This was repeated at two other patches at Cape Banks at a different date; patches used at each date were approx. 15 × 15 m and separated by at least 25 m. In this experiment, as in all following, the surface of the rock was relatively smooth and contained small pits/depressions about the size of 5–10 limpets. The null hypothesis that the proportion of new limpets in old resting sites would not differ between plots cleared of limpets and control plots, and that this would not differ between patches and/or times, was tested using ANOVA, with the assumption of homoscedasticity tested using Cochran's *C* (Underwood, 1997). Non-significant factors ($P > 0.25$) were eliminated from the ANOVA to increase the power of tests above (Underwood, 1997).

2.2. Experiment 1: previous occupancy predicts location and size of incoming limpets

The pilot experiment did not take into account local abundances of limpets and did not test for differences in sizes between new limpets and the limpets that had previously occupied their resting sites. Therefore, we repeated the pilot experiment in each of the two patches at Cape Banks with a set of control and removal plots ($n = 10$) being created as above, photographed at initiation (time 1) and three days later (time 2). Later, a person not associated with deployment of the plots scaled each photograph to the size of the 50 × 50 quadrat in the image and scored the presence and size of limpets. The standard quadrat frame was also marked with a millimetre scale using adhesive measuring tape. The scaled frame enabled us to plot the Cartesian coordinates of each limpet in the quadrat using the peak on the shell

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