THE BEHAVIORAL ECOLOGY AND TERRITORIALITY OF THE OWL LIMPET, *LOTTIA GIGANTEA*

by

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A DISSERTATION

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Territoriality, defined as an animal or group of animals defending an area, is thought to have evolved as a means to acquire limited resources such as food, nest sites, or mates. Most studies of territoriality have focused on vertebrates, which have large territories and even larger home ranges. While there are many models used to examine territories and territorial interactions, testing the models is limited by the logistics of working with the typical model organisms, vertebrates, and their large territories.

An ideal organism for the experimental examination of territoriality would exhibit clear territorial behavior in the field and laboratory, would be easy to maintain in the laboratory, defend a small territory, and have movements and social interactions that were easily followed. *Lottia gigantea*, the owl limpet, is just such a model animal. With a small territory (< 900 cm^2) and slow movements (3 mm/min), the interactions of several *L. gigantea* can be continuously and simultaneously monitored.

Using time-lapse photography, experiments were conducted to observe behaviors of *L. gigantea*, ranging from how *L. gigantea* form home ranges to how territorial *L. gigantea* interact. *Lottia gigantea* formed home ranges within four weeks, returning to a home scar after each foraging cycle. To determine whether *L. gigantea* returned to areas with greater food resources, three different algal density treatments were used, and individuals were monitored to see which tiles they frequented the most. *Lottia gigantea* actually avoided areas with a thick algal covering, potentially due to the loss of suction they experienced while moving across algae. When *L. gigantea* established territories, home ranges overlapped considerably. Two individuals were placed in one arena, under the assumption that a dominance hierarchy would be established. Dominant status was predetermined, and in four of the seven dyads both individuals were evasive. When subjected to territorial encounters for two weeks, *L. gigantea* avoided areas where they experienced agonistic losses. Mucus may serve as an olfactory cue to define territorial boundaries. Individuals avoided tiles with conspecific's mucus more often than tiles with self-mucus or no mucus.

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CHAPTER I

GENERAL INTRODUCTION

Territorial behavior occurs in several patellogastropoda species, primarily *Patella longicosta*, *P. caerulea* and *Lottia gigantea* (Underwood 1979, Branch 1981, McQuaid & Froneman 1993, Keasar & Safriel 1994). Experimental studies have focused on how limpets maintain their food source (Maneveldt & Keats 2008). Territorial limpets garden, altering and maintaining the biofilm found in the rocky intertidal. In addition to gardening, territorial limpets home, returning to a fixed location after each foraging cycle. Work done on the owl limpet, *Lottia gigantea,* a prosobranch gastropod found in the upper intertidal zone of the west coast of North America, has examined both the effect of territoriality on a food source and the ritualized territorial behavior itself (Stimson 1970, 1973, Wright 1982, Wright & Shanks 1993, Shanks 2002).

Gardening

Limpet gardening, or grazing in a select area to increase or modify the food supply, has been observed in patellid limpets (Branch 1971, 1975, 1976, 1981, 1992, Ridgeway et al. 1999, Plaganyi & Branch 2000). Gardening is a foraging strategy used by grazers where the algal assemblage is altered to benefit the grazer. Gardening is linked to territoriality; if an organism is a gardener, it must somehow maintain its food supply and keep intruders out. *Patella longicosta* and *P. tabularis* have demonstrated territorial tendencies, protecting their specialized gardens of *Ralfsia verrucosa* (formerly *expansa*) from intruders (Branch 1971, 1975, 1981; McQuaid & Froneman 1993).

McQuaid and Froneman (1993) removed *P. longicosta* from territories and found that *R. verrucosa* was overgrown by *Ulva* sp. (green foliose algae) in areas where all limpets were excluded. In areas where non-territorial limpets had access to the territories, *R. verrucosa* was completely eaten. *Scutellastra (Patella) cochlear* also occupy areas with specialized gardens of red algae and are able to fertilize gardens with nitrogenous excretions (Plaganyi & Branch 2000).

Homing

Homing behavior has been well documented in limpets, but no studies have looked at how territorial behavior is related to homing (Breen 1971, Hartnoll & Wright 1977, Little & Stirling 1985, Chelazzi et al. 1994, Santini & Chelazzi 1996, Ocana & Emson 1999, Davies et al. 2006). Homing gastropods are those that return to the same location, a home scar, after each foraging excursion (Villee & Groody 1940, Frank 1964, Cook et al. 1969). The mechanisms by which territorial limpets return to their home scar after foraging in their territories are unknown. Moreover, the foraging pattern may influence energy and time budgets.

Territorial Behavior in the Field

Territorial defense has been studied in *Patella longicosta*, a South African limpet species. Branch (1975) removed *P. longicosta* from rocks and transplanted them into *P. longicosta* gardens while the territory holder was out feeding. Upon return and contact with the intruder, the resident touched the intruder with its tentacles and the resident pushed the intruder off the garden. The intruder continued to flee despite not being pursued.

Recently, *P. barbara* were found to exhibit territorial behavior on the south and east coasts of South Africa, but not on the west coast (Ridgeway et al. 1999). If the limpet gardened, the individual was considered territorial. Gardens were measured and garden size was correlated with limpet size. This distributional variation in territoriality could possibly be explained by nutrient level since productivity is low on the east coast of South Africa (Ridgeway et al. 1999).

***Lottia gigantea* Territorial Behavior**

Most studies of limpet territorial behavior have been done on *Lottia gigantea*. Ricketts et al. (1985) reported that *L. gigantea* actively defended a territory (approx. 1000 cm^2) of algal film. Stimson (1970, 1973) speculated that territoriality evolved in *L. gigantea* as a means to maintain a food source by a large grazing organism. Stimson first marked 64 *L. gigantea* and measured their positions biweekly for five months. He also stained rocks to determine if *L. gigantea* remained in distinct grazed areas. *Lottia gigantea* removed both the stain and algae while grazing and radular marks were present on the grazed rocks. *Lottia gigantea* did not leave their territories, which averaged 900 cm^2, and the size of the area was proportional to *L. gigantea* size. *Lottia gigantea* established a territory in two weeks and the algal film was present only when *L. gigantea* were present.

Stimson also noted *L. gigantea* behavior in staged and unstaged encounters. When a resident limpet encountered an intruder, conspecific or not, it engaged in a "push and pursue" action, thrusting its shell under the intruder and moving its foot forward, pushing the intruder. It either dislodged it or continued to push until the intruder was expelled from the resident's territory. *L. gigantea* responded to predators, competitors for space, and competitors for food (Bullock 1953, Stimson 1970).

Stimson (1973) manipulated *L. gigantea* in the field and found that territory size varied with season, *L. gigantea* density and food supply. Territories were larger in early spring than late spring. When territories were smaller, *L. gigantea* had little growth. Territory size was the smallest where *L. gigantea* were the most abundant yet territories were larger when algae were less abundant. Territories touched, but did not overlap, as evidenced by narrow, ungrazed strips between territories. Solitary *L. gigantea* expanded their territories when algae were sparse and lived at higher density when food was abundant. Solitary *L. gigantea* also maintained larger territories than grouped ones, possibly because the grouped individuals were subjected to more frequent grazing intrusions.

Wright (1982) tested Stimson's 'push and pursue' response in the field and found that *L. gigantea* exhibited ritualized behavior. Rather than pursuing an intruder to the outskirts of its territory, a resident limpet would initially contact the intruder with a push, but the latency period of the resident was found to be longer than that of the intruder. The intruder quickly turned and retreated before the resident could react. The evasion response occurred when the intruding limpet turned 90° away from the resident and its speed was greater than that of the resident. It was also determined that residency trumped size; if a small resident limpet encountered a larger intruding limpet, the intruding limpet would still respond evasively. Wright concluded that the resident's response, that is its failure to pursue an intruder, implied an inherent knowledge of territorial display.

In the lab, Wright and Shanks (1993) were able to 'train' *L. gigantea* to display either territorial or evasive behavior. A subject limpet underwent either an agonistic victory (the cephalic tentacles of a stimulus limpet were first exposed to the subject and then removed) or a defeat (the stimulus limpet 'pushed' the subject limpet). They examined whether aggressive experience was dependent on previous experience even in the absence of extrinsic cues. Territorial-trained limpets had territorial behavior while limpets that received defeats were evasive.

Scope and Objectives of This Dissertation

The primary objective of my dissertation project was to look at the behavioral ecology of *Lottia gigantea*. My second objective was to examine some general questions about territoriality using *L. gigantea* as the model organism.

Prior to conducting experiments, I first had to develop methods to keep *L. gigantea* alive and healthy in the lab and ensure that time-lapse photography could be used to examine territorial behavior of *L. gigantea*. I conducted a preliminary study to determine whether *L. gigantea* was a suitable organism to study territoriality while testing the time-lapse system (Chapter II).

Once I established that *L. gigantea* is a good organism for long-term studies, I ran a month-long experiment to determine how *L. gigantea* establishes home ranges. I did this by placing individuals in separate arenas and monitoring their movements for a month (Chapter III).

A model by Stamps and Krishnan (1999) predicts that individuals should favor areas with a greater food source. In Chapter IV, I tested whether a limpet would frequent areas with greater food density more than areas with low food density. The results suggested another experiment to examine limpet tenacity (an organism's ability to stick the substratum) at different food densities.

After determining how *Lottia gigantea* established home ranges, I studied territory formation and territorial behavior. In Chapter V, I examined interactions among individuals of similar size. Stamps and Krishnan (2001) predicted that territory exclusivity is based on the degree of escalation in agonistic encounters. A fight leads to more exclusive territories, whereas chases produce overlapping home ranges. I placed two individuals in one arena and monitored these for six weeks to look at interactions and territory formation.

Lottia gigantea were then tested to see if they could learn to avoid areas where they experienced agonistic encounters. I subjected *L. gigantea* to staged agonistic losses using the training techniques employed by Wright and Shanks (1993), as detailed in Chapter VI. Over the course of two weeks, individuals were subjected to agonistic losses and their behavioral changes were assessed.

In the field, territorial *L. gigantea* do not pursue intruders past the edge of their territories. I speculated that limpets may use mucus to mark territory boundaries. I explored whether individuals differentiated tiles with their own mucus from tiles with mucus from another individual (Chapter VII). After two weeks of territory establishment, tiles from two separate territories were switched, then individual behavior was monitored. To assess the influence of algae on mucus-covered tiles, I conducted an experiment where none of the tiles had algae on them. Tiles in individual arenas were switched with tiles from one of three treatments:tiles with no mucus, tiles with a limpet's own mucus and tiles with another individual's mucus.

The main goal of my dissertation project was to study the behavior of *L. gigantea* in a controlled laboratory setting. In Chapters II-IV the focus was on how *L. gigantea* establishes home ranges, while Chapters V-VII I examined territorial behavior.

CHAPTER II

METHODS FOR LONG-TERM MAINTENANCE AND MONITORING OF THE OWL LIMPET, *LOTTIA GIGANTEA*

Introduction

Animals form territories for a variety of reasons, ranging from mate selection to resource acquisition. Territorial behavior has been examined in an array of animals, from large mammals to invertebrates (Higuchi & Hirano 1989, Bonaventura et al. 1992, Polak 1993, Burford et al. 1997, Hernandez & Laundre 2003, Eason & Switzer 2004, Bowen et al. 2008, Bo et al. 2010, Newey et al. 2010). Most territorial studies use large organisms as models, but since these animals generally have large territories, they are difficult to track. In addition, the tracking is usually over a three dimensional surface. Even small invertebrates such as insects have three-dimensional territories. Moreover, the behavior of such organisms may be complex, as is the case with bee foraging (Hassell & Southwood 1978, Brockmann 2001, Raihani et al. 2008, Kroiss et al. 2010, Stelzer et al. 2010). Since it is difficult to observe large individuals forming territories in the field, most studies only look at interactions once territories have formed. Maynard Smith's game theory (1976, 1979) has served as a paradigm for examining territorial interactions, but newer models challenge the paradigm (Gordon 1997, Stamps & Krishnan 1999, Sih & Mateo 2001, Stamps & Krishnan 2001, Switzer et al. 2001, Morrell & Kokko 2003, Lopez-Sepulcre & Kokko 2005, Morrell & Kokko 2005, Kokko et al. 2006). Maynard Smith's theory suggests that the 'winner takes all' in territorial interactions; in other words, the winner acquires or maintains its territory. Stamps and Krisnan (1999) propose that an individual may acquire territory by being persistent even in situations where the persistent individual loses. The Stamps and Krishnan model focuses on how territories are formed and suggests that territory formation may result from spatially-based learning. Individuals are able to assess areas that are suitable for territory establishment based on prior interactions. These new models have yet to be thoroughly tested.

As mentioned above, a large animal with a large home range makes it challenging to experiment with territory formation. A more practical organism would have distinct territorial behavior, be small enough to establish territories in the lab on a two dimensional surface, and would have behavior that could be easily followed. *Lottia gigantea*, the owl limpet, is an ideal organism with which to study territorial behavior under controlled conditions in the laboratory. It has distinct territorial behavior, but can be maintained in the laboratory and requires less than 900 cm^2 to establish a territory (Stimson 1970). In addition, *L. gigantea* is a homing limpet, returning to a home scar after each tidal cycle or foraging event (Wells 1917, Galbraith 1965). In the laboratory, *L. gigantea* forms a home scar within two weeks and remains within its territory, even when there is additional space available (pers. obs.). This homing instinct makes it easy to restrict *L. gigantea* to a designated area and monitor all movements and behaviors using time-lapse photography. *Lottia gigantea* can be maintained on a two-dimensional surface, such as an unglazed terra cotta tile, as long as the surface promotes algal growth. Like other limpets, *L. gigantea* are microphagous generalist grazers that eat biofilms and macroalgal propagules, a diet that can be easily maintained with a flow-through sea water system (Underwood 1979, Hawkins & Hartnoll 1983).

Lottia gigantea is a prosobranch gastropod belonging to the family Lottiidae (Gray 1840) (Lindberg 1986). It ranges from Neah Bay, Washington to Baja California

(Ricketts et al. 1985), but is most common south of Bodega Bay, California. *Lottia gigantea* is found in the high mid and upper intertidal zones on exposed and semi-exposed rocks. This species is one of the largest west coast intertidal limpets, growing up to 10 cm in length. The species is protandrous, switching from male to female, with most females being large and males being smaller. *Lottia gigantea* is a sequential hermaphrodite; simultaneous hermaphrodites have seldom been found (Wright & Lindberg 1982, Lindberg & Wright 1985). *Lottia gigantea* reproduces once each year via broadcast spawning (Daly 1975). Larger female *Lottia gigantea* are territorial, defending an area no larger than 900 cm^2 (Stimson 1970, 1973, Wright 1982). The territorial behavior of *Lottia gigantea*, while complex, is consistent and similar in the field and the laboratory. A territory holder will retract its foot and then push an intruder to the periphery of its territory or knock the intruder off the substrate (Wright & Shanks 1993, Shanks 2002). The intruder grazes on the territory until encountered by the territory holder, then quickly (1.07 mm/s compared to its normal speed, 0.05 mm/s) exits the territory. When encountered by the territory holder the intruder exhibits evasive behavior by turning 90° away from the other limpet and retreating (Wright 1982).

While limpet foraging behavior has been extensively examined in South Africa, Europe and the United States (Hartnoll & Wright 1977, Branch 1981, Chelazzi et al. 1998, Williams et al. 1999, Espinosa et al. 2008, Johnson et al. 2008, Noel et al. 2009), limpet territoriality has received less attention (Stimson 1970, 1973, Branch 1975, 1976, Keasar & Safriel 1994, Ridgeway et al. 1999) and little experimental work has been done (Wright & Shanks 1993, Shanks 2002).

The goals of this study were twofold: 1) ensure that *L. gigantea* could be maintained for long periods in the laboratory and, 2) to set up a time-lapse system for examining territorial behavior. The techniques developed in this paper allowed *L. gigantea* to survive and grow in the laboratory for a minimum of eight months, adequate time to set up long-term experiments. All movements of all individuals were tracked with the use of time-lapse photography on a two dimensional surface and territorial behavior was recorded.

Materials and Methods

Animal Husbandry

The laboratory setup was based on earlier work done by Wright and Shanks (1993) and by Shanks (2001). In the present study, limpets resided in sea tables, on unglazed terra cotta tiles, which promote algal growth (Figure 2.1). Initially, 15.4 by 15.4 cm tiles were used. The tiles were placed on a piece of plywood which was held at an angle of 70°. The tiles were surrounded by an Astroturf™ fence; *Lottia gigantea* do not cross an Astroturf™ barrier (Wright and Shanks 1993). The tiled arena was 1 m^2. Limpets were maintained under lights on a 12:12 light dark cycle to promote algal growth and mimic natural conditions. The lighting system was a high-output fluorescent fixture using four 54 watt high output fluorescent lights, two yellow and two blue (General Electric, yellow-4700 lumens, 3000 K; blue-4370 lumens, 6500 K). The light fixture was covered with a clear acetate film to decrease moisture and salt water damage and mounted parallel to the tile arena, ensuring that all tiles received the same amount of light. The tides were mimicked by installing a Gilmour water timer (Model 9400) to the flow-through sea water system. Water flowed for four hours, twice a day, simulating a semidiurnal tidal cycle. To create waves, a dump tank filled with water splashing the limpets every 30 seconds. The dump tank was made from a PVC pipe cut in half, with a weighted axle, so it filled with water, dumped and then righted itself.

Figure 2.1. Laboratory Setup. Nine *Lottia gigantea* were placed on a 1 m^2 arena composed of unglazed terra cotta tiles. The numbers were the identifiers for each individual. The dump tank was located above the setup. The dump tank splashed the limpets with water at a regular interval, mimicking the high tide. The dump tank ran for four hours, twice a day. One tile side=15.24 cm

Time-lapse Photography

The preliminary study was photographed using a Nikon Coolpix 5700 digital camera attached to a Digisnap time-lapse controller (Harbortronics, inc., model 2100). The camera was hung from a beam in waterproof housing above the setup. To ensure adequate tracking of all limpet interactions for the preliminary study, photographs were taken every minute. To track individual limpets, tags were attached to shells with epoxy. To visualize their interactions, most of which occurred at night, a red light was used to illuminate the system in the dark. A similar illumination technique has been used in various limpet experiments and does not alter their behaviors (Gray & Hodgson 1998, Ocana & Emson 1999, Davies et al. 2006).

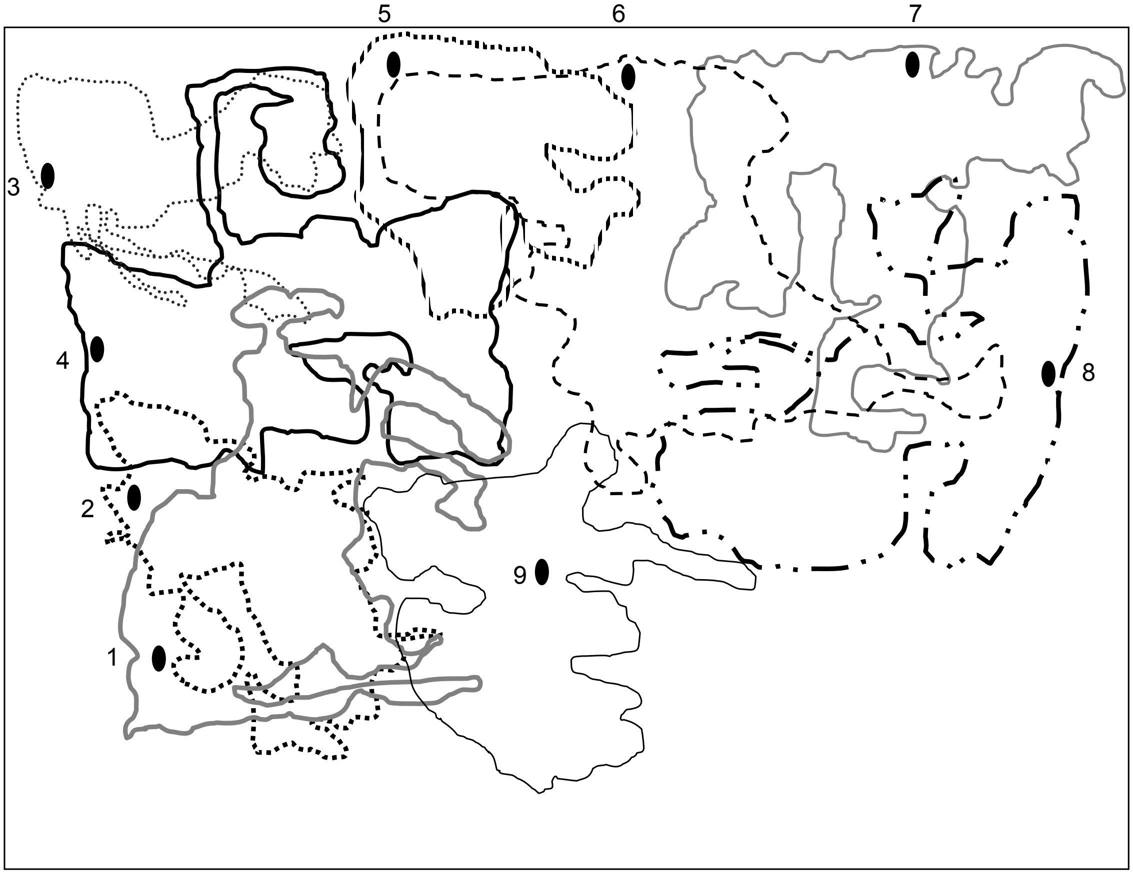
Nine *L. gigantea* were collected from Carmel, California in July 2006. The limpets ranged in size (measured in length along the maximum axis) from 22 - 46 mm. Shell length is the standard for measurement of limpet size (Stimson 1973, Pombo & Escofet 1996, Kido & Murray 2003). In October 2006 a weeklong test of the time-lapse system was conducted. The limpets were filmed for an average of 8 hours at night, during their active period at the mock high tide. These nine individuals did not move during the daytime, but other populations in the laboratory moved during both the day and night high tides. To ensure all movement was tracked, the limpets were filmed during the 4 hours when the dump tank was in operation (mock high tide) and 4 hours after mock high tide had ceased. The photographs were then converted into an .avi file using MakeAVI software (http://sourceforge.net/projects/makeavi/). AVI files were converted into Quicktime videos with AVS Video Converter 6.2.

To track limpet movements and monitor territorial behavior, a piece of clear acetate was placed over a computer screen and each individual's movements were traced and calculated to scale using a rolling distance measuring tool to obtain the path length for each foraging excursion. Each individual's home range was summed by combining its foraging path over 7 days. The area of the home range was determined by overlying all 7 paths of each individual and tracing only the outside lines. The area was calculated by cutting out the areas from the acetate map and weighing them to the nearest 0.01 g, using a ratio to convert the weights to areas (Shanks 2002). To determine exclusive territorial area, only the area exclusively traversed by an individual was cut from the acetate once the home range area was determined.

Results

The summer of 2006 was spent ensuring a successful setup for long-term maintenance of *Lottia gigantea*. Nine limpets were collected in July 2006 and all individuals survived for eight months, until the timer on the water system failed. Limpets in the experimental arena displayed the same foraging, homing and territorial behaviors as observed in the field (Stimson 1970, 1973; Wright 1982). In the field, *Lottia gigantea* forages on the high tide, usually at night, returning to its home scar during low tide (Stimson 1970). In this lab study, territorial individuals established territories and demonstrated territorial behavior, meaning they pushed intruders out of their territories. The limpets established home scars and territories within three weeks on the artificial setup. The arena was large enough that individuals could establish non-contiguous territories, but they established territories in three-quarters of the arena and territories were contiguous (Figure 2.2). The territorial individuals returned to the same location after each foraging cycle and the longest distance traveled by any individual was 48.6 cm from its home scar.

Figure 2.2. Home ranges of nine individuals. Black ovals indicate individual home scars, locations individuals would return to after each foraging cycle. Individual #2 appeared to be non-territorial as it responded evasively in every encounter. Individual #3 was potentially evasive, but only had one interaction. The remaining individuals displayed territorial behavior in at least one interaction.



From the videos compiled by the time-lapse photographs, I delineated the limits of each animal's home range and exclusive territory. The foraging path of each individual was plotted each time an animal moved. Foraging paths changed each day such that they tended to forage new areas each day and over several days' foraging paths, the combined foraging paths formed a pattern resembling a flower petal (Figure

2.3). The outside edge of the combined foraging paths was considered the home range. As in the field, home range area was significantly correlated with limpet size (Figure 2.4) (Stimson 1970). Exclusive territory area was considered the total home range area minus the area shared by other individuals. The average exclusive area was 356.13 cm^2 $\pm$ 83.74 (45.07% $\pm$ 10.30 of the total home range). Five of the 9 individuals had >40% defended as exclusive area.

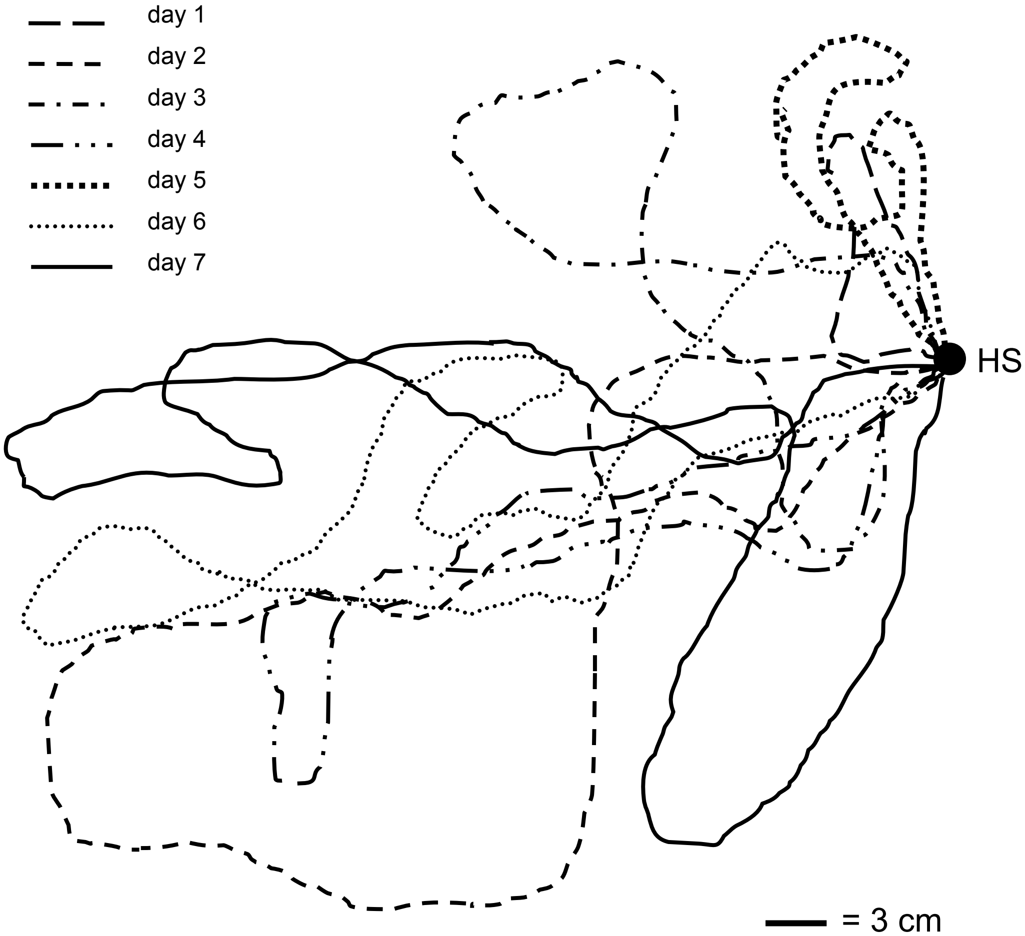


Figure 2.3. Daily foraging paths of one individual (# 8) over seven days. HS=home scar.

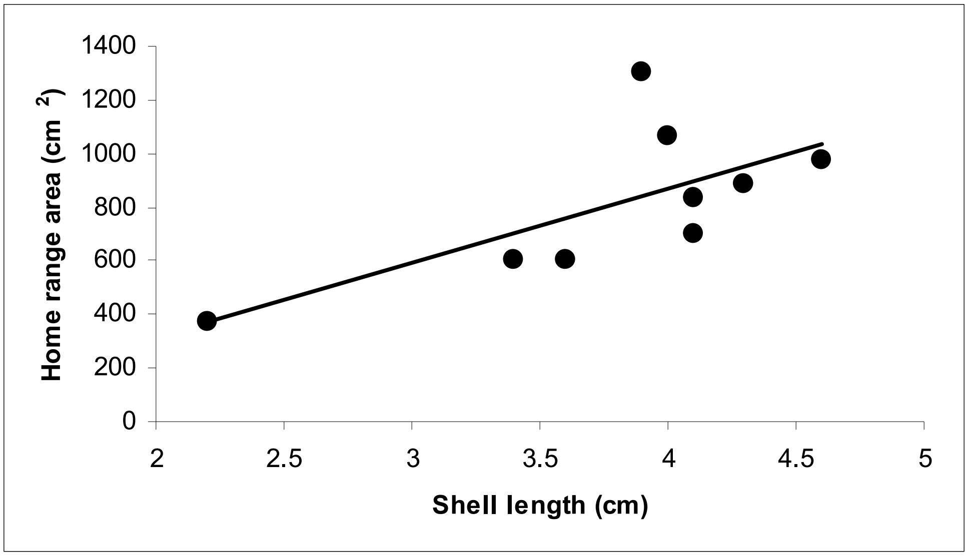


Figure 2.4. Limpet length as a function of home range area over the course of seven days (Regression, $R^2=0.467$, F=6.122, n=9, $p<0.05$). Larger individuals traversed more area than smaller individuals.

Individuals were classified as territorial or evasive. Territorial animals were considered individuals who pushed and pursued intruders out of their territories. Evasive individuals ‘quickly’ retreated, turning > 90º away from the point of contact with another individual. Seven individuals demonstrated territorial behavior while one individual was clearly evasive. One additional individual appeared evasive, but there were not enough interactions to confirm this behavior. The evasive and potentially evasive individuals were the smallest individuals, 22 mm and 34 mm, respectively. The average length for the 9 individuals was 38 $\pm$ 2.3 mm (mean $\pm$ SE). The average growth rate of the territorial animals was 0.9 mm/month (SE = 0.05, n=7) while the evasive animals did not grow (n=2).

There were 23 behavioral interactions when one individual made contact with another during the 7 day period (Table 2.1). Territorial interactions occurred when one individual pushed and then pursued the intruder, while the intruder turned away from the pursuer and retreated. Twenty-one interactions were territorial and two were potentially territorial. During the potential territorial interactions, the initial push was not photographed, but in each case one individual could be seen moving rapidly away from the probable point of contact. Seven of the nine individuals defended a territory. When an intruder encountered a territory holder, the territory holder pushed the intruder and pursued it to the periphery of its territory. The intruder turned away from the territory holder and ‘quickly’ exited the area. These behaviors were consistent with those observed in the field (Wright 1982, Stimson 1970). Eleven of the 23 interactions involved the evasive limpet (Individual #2). Individual #2 consistently intruded on adjacent territories and, when contacted by the territory holder, displayed evasive behavior and was chased from the territory. Intruders were caught about 70% of the time they invaded a territory. Individual #3 appeared to be evasive, but only had one interaction with another limpet. Established territory holders generally did not interact, even when their movement trajectory was towards another individual. One individual was an exception and routinely challenged its neighbors. The eleven remaining interactions involved one individual territory holder (Individual #6). Individual #6 was territorial when it was near its home scar (two interactions), but evasive when it encountered neighboring territory holders in areas where their home ranges overlapped.

Table 2.1. Number of interactions. Twenty-one interactions were territorial and two were potentially territorial. The initial distinct shove of a territorial interaction was not captured on film for one interaction between individuals 7 and 6 and one between individuals 9 and 6.

Territorial individual	Evasive individual	# of Interactions
1	**2**	8
4	**3**	1
4	**2**	2
5	**6**	3
6	**5**	2
7	**6**	2
8	**6**	3
9	**2**	1
9	**6**	1

Discussion

The purpose of this study was to investigate the possibility of using *Lottia gigantea* as a model organism for experimental laboratory studies of territorial behavior. A model organism should be relatively easy to maintain in the laboratory and its behavior in captivity should be very similar or identical to that seen in the field. It should be possible to follow their behaviors continuously, observe enough individuals to obtain an adequate sample size, and manipulate the behavioral interactions. All of these criteria were met; *L. gigantea* had consistent behavior that appeared identical to normal field behavior, all behaviors of all individuals were captured with the time-lapse system and individual interactions were observed. The use of tiles allowed for easy manipulation of the substratum and of individuals on the tiles.

An additional advantage of *L. gigantea* as a model organism is that individuals can be “trained” to be territorial or evasive (Wright and Shanks 1993). By mimicking territorial encounters, Wright and Shanks were able to modify *L. gigantea* behavior. The cephalic tentacles of the stimulus limpet were held in contact with the cephalic tentacles of the moving subject limpet until the subject limpet began to display a response, resulting in either an agonistic victory or a loss. In the case of a victory, the stimulus limpet was removed, but in the case of a loss, the stimulus limpet was used to push the subject limpet at a consistent and forceful rate to the edge of a tile. When an individual experienced a loss, it demonstrated evasive behavior in subsequent interactions and if it experienced a win, it was territorial. Wright and Shanks (1993) also examined if the behaviors could be switched with additional training. Individuals switched their behaviors, but it took longer for evasive individuals to become territorial.

In the current study, *L. gigantea* were maintained in healthy condition for eight months and their demise was due to equipment failure over a weekend. In subsequent studies, *L. gigantea* remained alive and healthy for over a year. *Lottia gigantea* has been found to grow 0.26 mm/month in the field (Stimson 1973). All nine individuals grew a few millimeters in the four month period they were monitored, as evident by new shell growth. This indicated that they were healthy and had adequate food, since they grew faster than individuals in the field.

The successful maintenance of *L. gigantea* in the laboratory was probably dependent on two factors, a healthy biofilm on which they could feed and a fairly realistic tidal system. A sufficient and healthy biofilm grew on the porous unglazed terra cotta tiles and the flow-through seawater system seeded the tiles with microscopic algae. Since *L. gigantea* do not survive when submerged for long periods, re-creating a splash zone with the dump-tank created a more realistic environment in the laboratory and insured their longevity. In addition, *L. gigantea* typically only move when being splashed with water, so their movements were controlled by the duration of the mock high tide.

A time-lapse system was tested to track all individuals, see all interactions, including territorial behavior, and define home ranges and territories over seven days. All interactions were recorded, the individuals displayed the same distinct territorial behavior as seen in the field and limpet length and territorial area were correlated. A picture every 60 seconds was sufficient time to see territorial behavior, even in the case where the initial shove was not seen, the behavior was evidenced by the quick retreat of the intruder.

A “dear enemy” effect may be at work since there were few aggressive interactions between territory holders (Temeles 1994). Territory holders were seen to approach the periphery of their territories, then abruptly turn when they encountered the border of their neighbor’s territory. While there was adequate divisible space for individuals to form non-contiguous territories, the individuals established contiguous territories and all of the boundaries overlapped. In the field, *L. gigantea* territories are often contiguous, but interactions are not frequently seen, suggesting that established territory holders avoid each other. Neighboring territories may decrease intrusions from non-territorial *L. gigantea* and other limpet species. *Lottia gigantea* remove both space and food competitors from their territories (Stimson 1970), so by having additional conspecific neighbors they increase the number of barriers to non-conspecific competitors surrounding their territories.

Limpets are important herbivores and space holders in the intertidal zone. Their behavioral ecology may have important impacts on their population ecology and, hence, the structure of the community. Zonation in the rocky intertidal is determined predominantly by biotic factors in the lower zones (Underwood 1979, Branch 1981); distribution and succession in the rocky intertidal can be greatly affected by grazing gastropods. A larger gastropod grazing on macroalgal propagules can prevent the succession of competitively dominant algae. Territorial limpets can bulldoze sessile invertebrates from their established area; in territorial studies, *L. gigantea* prevented or decreased mussel encroachment on territorial sites (Stimson 1973). In both this study and others, *L. gigantea* appears to be a prudent grazer, much like *Patella spp.* (Ridgeway et al. 1999, Plaganyi & Branch 2000, Shanks 2002). This prudent grazing can lead to individuals essentially cultivating algae that would normally be overgrown by more competitive seaweed. By studying *L. gigantea* behavior, we can surmise how territorial behavior plays a role in rocky intertidal community structure, while gaining insight into *L. gigantea* foraging behavior.

The motivation for this study was to create a system for testing territorial behavior models in the laboratory for long-term studies. This preliminary study was conducted in 2006 and the setup is still being used in 2011, suggesting that it is a viable option for studying territorial behavior on a small scale. Improvements have been made since the preliminary study. The tiles have been cut into quarters, making 7.6 x 7.6 cm squares. The smaller tiles make it easier to move individuals around the arena and manipulate the shape and arrangement of the arena. The arena size was increased from one m^2 to 1 x 2 meters so that a greater number of individuals can be viewed at one time. The photographic interval was reduced from 60 seconds to 15 seconds, so all interactions could be viewed. One minute was too long and did not allow accurate observation of behavior; through trial and error, I determined that a 15 second interval allowed for accurate behavioral observations in subsequent studies. New observations have been made on *L. gigantea* behavior, ones that have the potential to explain not only *L. gigantea* behavioral ecology, but can also be applied to general territorial models. Examination of *L. gigantea* behavior has the potential to expand our knowledge of territorial establishment, territorial interactions and the 'dear enemy' effect.

Bridge I

In Chapter II, I described the *Lottia gigantea* husbandry and the time-lapse photography system that I used for all of my experiments. I did a preliminary study to begin looking at *L. gigantea* behavior and home range formation. In Chapter III, I delved further into *L. gigantea* home range formation.

CHAPTER III

LOTTIA GIGANTEA HOME RANGE FORMATION

Introduction

A home range can be defined as the area traversed by an organism that provides adequate resources for an individual to survive and reproduce (Burt 1943, 1966, Jennrich & Turner 1969, Wilson 1975, Schoener 1981, Dahle et al. 2006). Within its home range an animal may have a territory, an area that it actively defends. An animal may form a territory to protect a food source, nest site or mate. The definition of a territory is less clear cut; Maher and Lott (1995) found 48 different definitions of a territory when they reviewed the literature, depending on the researcher's focus (Fretwell & Lucas 1969, Kaufmann 1983, Boerger et al. 2008). Territorial definitions vary between behavioral and ecological functions. Behavioral definitions focus on the interactions between individuals whereas ecological definitions consider the consequences of territorial behavior (Maher & Lott 1995).

While there are models that examine how home ranges and territories are formed, it has been difficult to test them since the focus of studies has been on large vertebrates with large home ranges (Bacon et al. 1991, White et al. 1996, Lee & Su 2009). Home range analyses tend to examine what happens after a home range has been established, focusing on habitat use or the seasonal shifts in home range size ((Dahle et al. 2006, Novoa et al. 2006, Goettert et al. 2010). In addition, many studies must estimate size and shape of the home range since the subject organism is a vertebrate with a large range.

These estimates are not as accurate as actually determining the area covered (Mohr & Stumpf 1966, Jennrich & Turner 1969, Schoener 1981, Worton 1987, 1989).

For any given species, there are costs and benefits to establishing and subsequently defending a territory (Krebs & Davies 1993, Adams 2001). The establishment of a territory may define population spacing and have cascading effects that affect the ecological distribution of a species. Therefore it is key that home range/territory establishment of a species be understood. To define more accurately what a territory is and how it is formed, we require an organism with both a small home range that can be controlled in the laboratory.

Lottia gigantea, the territorial owl limpet, form small territories and move at speeds and over distances that can be easily tracked with time-lapse photography, making it feasible to study territory formation and test the accuracy of existing territoriality models. It is an herbivorous gastropod species found in the upper intertidal zone of the west coast of North America, that maintains and defends a territory. In the case of *L. gigantea*, territories are formed to protect a food source (Stimson 1970, 1973). Typically, territorial animals have large home ranges with smaller territories, but in the case of *L. gigantea*, its home range is equivalent to its territory.

As in territorial vertebrates, there are costs to both establishing and maintaining the grazing territory for the owl limpet. Costs come first in the seeking out of appropriate habitat, followed by exclusion of intruders and the continued defense of the territory. When a territory holder encounters an intruder, usually another limpet, it will retract its foot and shove its shell under the intruder in an attempt to knock it off the substrate (Wright 1982). If this method fails, the territory owner will push and pursue the interloper to the periphery of its territory. If the intruder is a sessile organism such as a mussel or a barnacle, *L. gigantea* will bulldoze it off the rock and create a clearing (Stimson 1970).

The purpose of this study was to examine how *L. gigantea* establishes home ranges. Since the home range of *L. gigantea* is equivalent to its territory, home range formation was considered potential territory formation. The goal was not to look at the maintenance of an established territory, but to determine the behavior prior to territorial defense in order to create a baseline for further studies. Stamps and Krishnan (1999) suggest that organisms will return to areas where they do not experience any agonistic encounters, thereby establishing a territory. Individual *L. gigantea* were placed in a mock-intertidal habitat in isolation and their movements and behaviors monitored. Individuals were monitored for 4 weeks, twice a day, during their active periods at simulated high tide. Limpets were provided with ample space in which to establish a home range and algal food resources to encourage the establishment of territories. Daily path lengths and the cumulative area visited were used as a proxy for the foraging territory.

Materials and Methods

Husbandry

Lottia gigantea were collected in Orange, California in May 2008 and transported to the Oregon Institute of Marine Biology in Charleston, OR. Individuals were placed on unglazed terra cotta tiles and kept in sea tables on a plywood frame tilted at a 70° angle from the horizontal. Limpets were exposed to waves for four hours, twice a day, to mimic a high tide period, similar to what they experience in the field. The waves were generated by a dump tank located above the plywood frame. The dump tank was connected to a flow-through sea water system; the dump tank filled with water, it tipped over, splashing the individuals with water and then righted itself with a counterweight. The limpets only moved during the high tides, which occurred every twelve hours. The "mock intertidal" was lit by four 54 watt high-output fluorescent lights, two yellow and two blue (General Electric, yellow-4700 lumens, 3000 K; blue-4370 lumens, 6500 K) placed above the frame on a 12:12 light:dark cycle which was similar to seasonal field conditions in the spring. The fluorescent lights promoted an algal biofilm to grow on the tiles. Limpets are microphagous grazers, feeding on the bacteria, microalgae and macroalgal propagules that grow in the rocky intertidal (Underwood 1979, Branch 1981, Hawkins & Hartnoll 1983). For complete husbandry details see Chapter II.

Experimental Setup

Ten *L. gigantea* of various sizes (30-46.5 mm) were held in isolation in the mock intertidal beginning on June 6, 2008 for four weeks. Because territory size is correlated with shell length (Stimson 1969), I calculated arena size by using Stimson's regression from the field. In this study, individuals $\leq$ 36 mm long were placed in arenas 500-700 cm^2 (composed of 9-12 tiles). Individuals > 36 mm were placed in 1170-1444 cm^2 size arenas (20-25 tiles). The arenas were larger than necessary for a territory, allowing the individuals to have ample divisible space to form territories (Stimson 1970). Isolation arenas were constructed by placing wooden fences over the tiles. I attached 6 cm long vertical dowels to the shells with epoxy, which prevented them from entering another arena when the dowel made contact with the fence (Figure 3.1). A home range is defined as the total area used by an individual, which can overlap with other home ranges, while a territory is the area used exclusively by one individual (Sih & Mateo 2001). Since each individual was placed in its own arena, the terms 'home range' and 'territory' are used here interchangeably. Although *L. gigantea* was not subjected to territorial interactions, it was assumed that individuals were potentially forming territories.

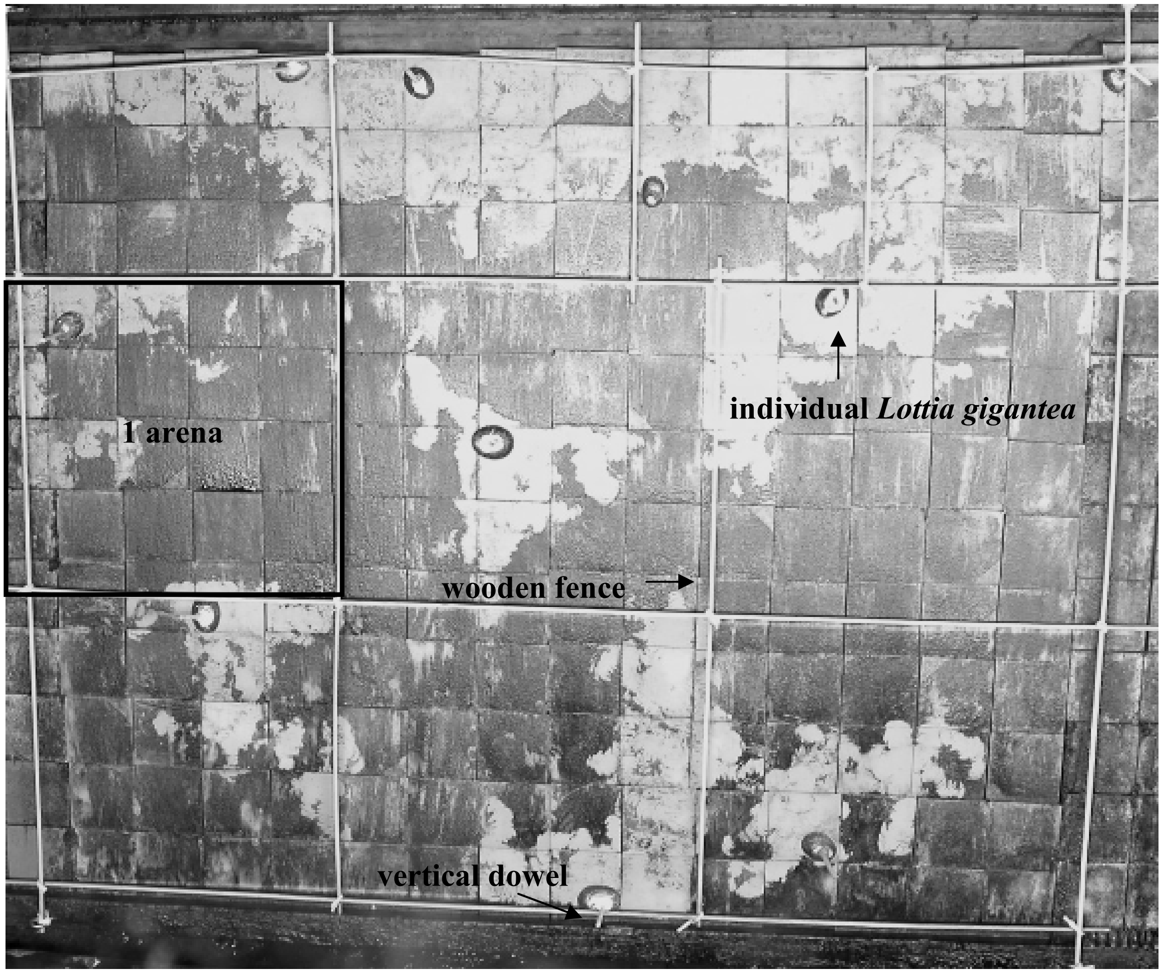


Figure 3.1. Experimental setup. Ten individual arenas were separated by the wooden fence, with one individual *Lottia gigantea* in each arena. The dump tank was located above the experimental setup. The lighter areas were where individuals had foraged. Each tile side=7.6 cm

Algal density was measured to ensure that the food source was evenly distributed on the experimental setup. Food availability was estimated by visual approximation, i.e., tiles were selected with a similar algal coating. Tiles were placed in the experimental setup 1.5 months prior to the start of the experiment. Chlorophyll samples were taken to confirm food availability by taking two random chlorophyll samples from each arena (n=20). I scraped a corner (~3.9 cm^2) of a randomly selected tile and used standard chlorophyll extraction techniques (Parsons et al. 1993). Samples taken before the experiment and after the experiment were measured in a fluorometer (TD-700 Laboratory Fluorometer, Turner Designs). Chlorophyll samples were taken after the experiment from both inside the territory (n=10) and outside the territory (n=10).

At the beginning of the experiment, individuals were placed in the middle of their respective arenas. Typically, *L. gigantea* only move when being splashed by water and do not begin moving until twenty minutes after first being splashed (Stimson 1970). During the high tide, a picture was taken every 15 seconds, for 5.5 hours and the limpets were photographed for four weeks using a Digisnap time-lapse controller (Harbortronics, inc., model 2100) attached to a Nikon Coolpix 5700 digital camera mounted above the experimental setup. Although the high tide lasted four hours, the extra 1.5 hours of footage at the end of the high tide was to ensure that all movement was captured. *Lottia gigantea* does not move until it is splashed by waves, but it will continue to move after splashing stops, but the substratum is still wet (Stimson 1970, Wright & Shanks 1993, pers. obs.).

Image Analysis

The pictures were converted to .avi movies using MakeAVI software (http://sourceforge.net/projects/makeavi/). AVI files were converted into Quicktime videos (AVS Video Converter 6.2) to be analyzed using Image J software (http://rsbweb.nih.gov/ij/). To track limpet movement a grid dividing the tiles into quarters was overlaid onto the videos. Individual location was scored every 10 frames (2.5 minutes), for 1320 frames per video (58 videos total), using ImageJ. The time spent on a tile was summed to determine where individuals spent the most time during their active periods and if they formed home scars. An individual was considered to be in a square if greater than 50% of its body was inside. The grid location was scored with a '1.' Transitions were scored when an individual was half on a grid line and each grid received '0.5' as a score. The location of each individual was summed for the four weeks they were filmed and mapped out to determine the number of tiles used. The total number of visits for the four weeks was 7294 ± 18 (average of ten individuals ± SE).

The location data were used to examine home scar establishment. A home scar is formed when a limpet returns to the same spot after each foraging event (Wells 1917, Underwood 1979, Chelazzi 1990). In this study, home scars were defined as tiles that limpets returned to after each active period. Individuals were considered as having formed a home scar if they spent 33% of their active time in the same spot over all active periods. As the home scar data were processed, it was determined that some individuals preferred two locations, so the home scar definition was expanded to include two spots. The limpets were filmed for 11 hours each day and were only splashed with water for 8 hours. Homing individuals were on their home scars for the first twenty minutes and last 1.5 hours of each filming session, which accounted for 33% of the footage.

The distance travelled per foraging excursion was measured by using the GroupedZ Projector plugin in ImageJ to stack all the pictures from each video into one superimposed image so the path each individual took was visible. The path was then traced for each individual and quantified. The cumulative foraging area of each individual was calculated every three days by tracing the outside parameter of the foraged area using ImageJ. The foraged area was easily visible as individuals scraped away the biofilm from the tile. Unscraped areas were brown while areas individuals traversed were the color of the tiles (Figure 3.2).

Statistical Analysis

Four response variables were analyzed following the 4-week experiment: total home range, formation of a home scar, length of forays and cumulative foraged area. I tracked individuals to determine the amount of time spent in each area of their arenas. From this I determined home range and home scar formation. I also determined how long it took to form a home scar. Regressions were used to compare limpet size (shell length) with final area and path length. ANOVAs were used to determine if individuals moved further based on when they moved the most (day vs. night) (SAS, version 9.2).

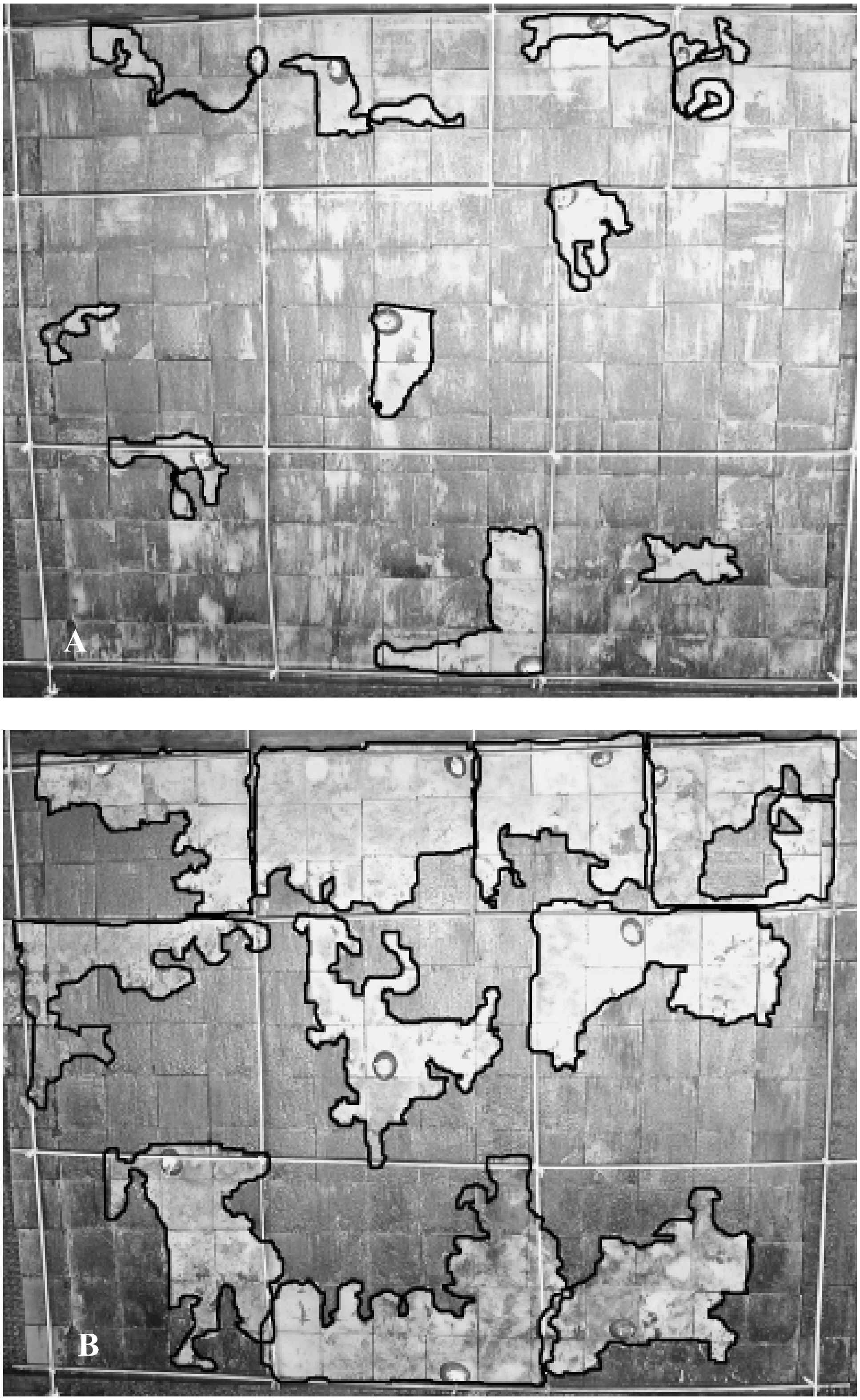


Figure 3.2. Cumulative foraging paths for A) day 3 and B) day 27. The paths were traced every three days and the areas were calculated using ImageJ.

Results

Prior to the experiment, the tiles visually appeared to have an even coating of algae on them and this was born out by the chlorophyll analysis; the average chlorophyll density on the randomly selected tiles from each arena was 3.28 ± 0.5 ug/cm^2. After the experiment, chlorophyll densities inside the territories were 0.63 ± .24 ug/cm^2 and 13.14 ± 1.4 ug/cm^2 outside the territories, indicating that territories indeed were foraging areas. The difference in chlorophyll concentrations between inside and outside foraged areas was significant (unpaired t test, $t=8.51$, $p<0.0001$).

The location data were compiled to determine the most visited and least visited areas of each arena. By the end of the third week, eight of the ten individuals formed home scars, locations they returned to after each foraging event. Three individuals formed a single home scar while the remaining six homing individuals preferred two locations rather than one home scar. Larger individuals tended to spend more time on their home scars (Figure 3.3). Of the two individuals that did not form home scars by the end of the third week, one individual had a home scar by the end of the fourth week while the other individual did not form a home scar after four weeks. The individual that did not form a home scar by the fourth week had a preference for two locations and spent 29% of its foraging time on them. The non-homing individual visited several areas with similar frequency, whereas homing individuals visited distinct locations (Figure 3.4).

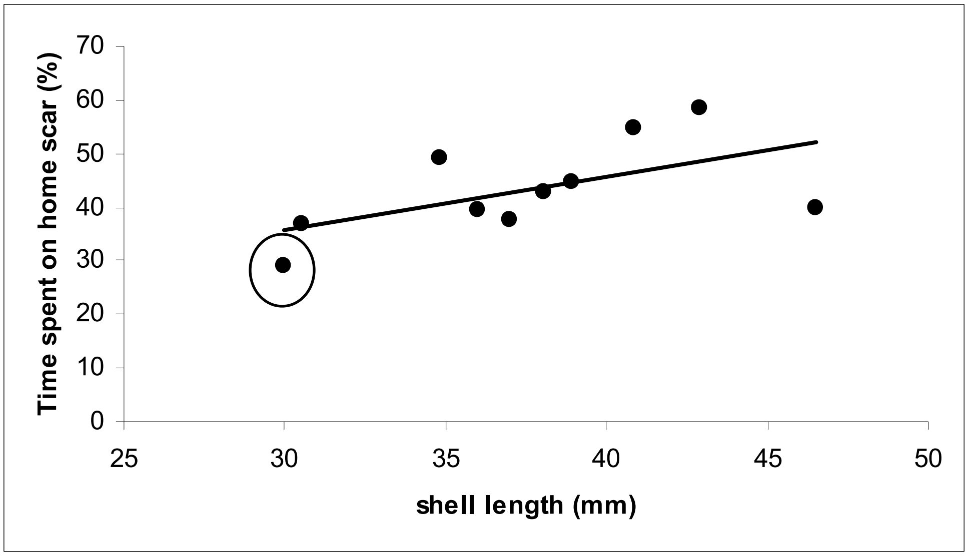


Figure 3.3. Time in residence on a home scar during the active period ("high tide") plotted against an individual's size (R^2=0.328, Regression, n =10, F=3.90, p=0.08). The smallest individual (circled) did not form a home scar, but was included in the data analysis since it spent 29% on the same area. Total time was based on when individuals were potentially active and foraging (i.e., "high tide"), which was 11 hours/day.

Total path length was measured for each individual, during each foraging cycle. Individuals preferred to move either during the day or night cycle. Four of the ten individuals moved more during the daytime high tide than at night. Individuals were compared to their preferred time of movement (day/night). Both time of movement (day or night) and individual were significant, but different individuals had different movement patterns, accounting for the significant interaction between the two factors (2-way ANOVA, n=10, F=23.19, p<0.0001). That is to say that whether an individual moved during the day or the night was based on individual behavior, not based on time of day. The period when an individual moved did not affect the distance traversed. The distance an individual moved was similar, regardless of day vs. night movement preferences (Table 3.1). When an individual preferred to move (day vs. night) was not based on size or homing behavior (Figure 3.5).

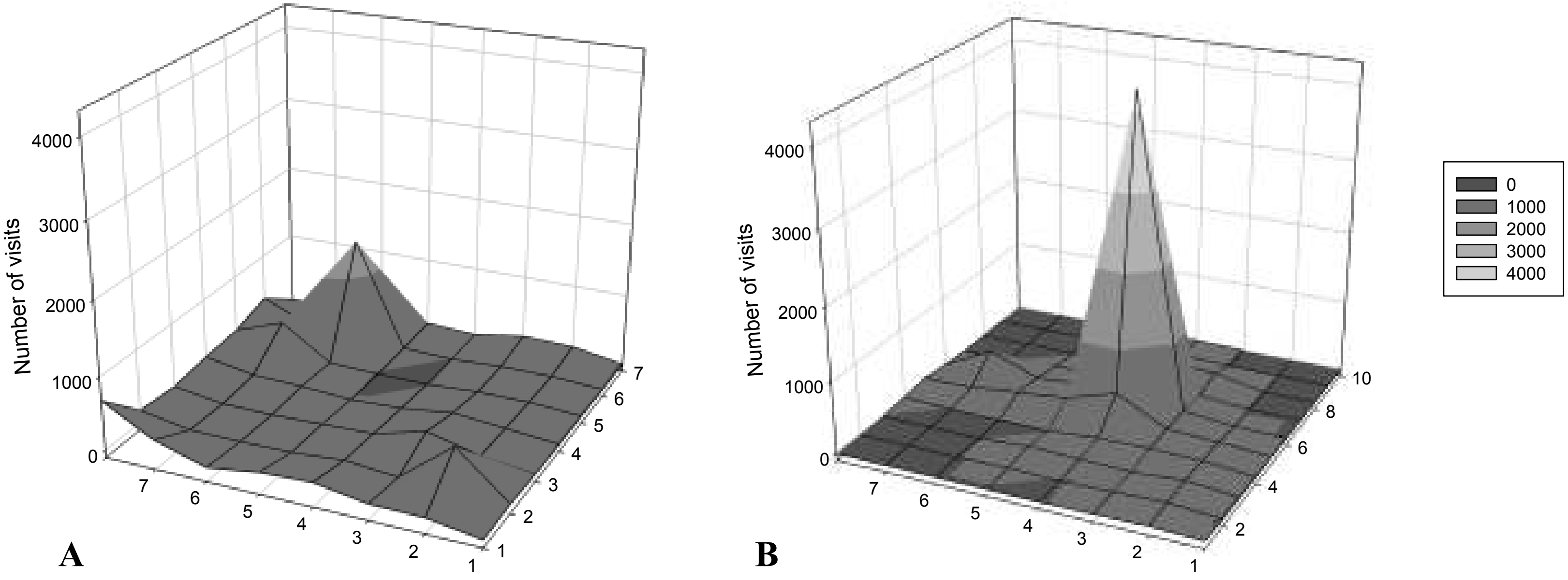


Figure 3.4. Space used by A) a representative non-homing individual and B) a representative homing individual. The 3D graphs represent the number of visits to each tile within the arena occupied by each individual. Peaks indicate tiles visited most frequently or for longest and are equivalent to a home scar when a peak accounts for > 33 % of an individual's foraging time. The individual on the left did not have one distinct home scar and visited more tiles with a greater frequency. The individual on the right formed a home scar where it spent 58% of its active period ("high tide" when it could forage) on its home scar. The horizontal axes represent the tile arena. The total number of visits for the four week experiment was 7294 ± 18 (average of ten individuals ± SE).

The path length for each individual was averaged for first nine days of the experiment and the last nine days. When the path length averages were compared, individuals moved greater distances at the end of the experiment (Unpaired t test, n=20, t=2.31, p<0.05).

Table 3.1. Average distance (cm ± SE) moved during a foraging event, based on when an individual preferred to move. The distance an individual moved was not different based on when the individual moved (one-way ANOVA, preferred tidal cycle-F=0.21, n=10, p=0.65; non-preferred, F=0.76, n=10, p=0.41). n=4 for day movers and n=6 for night movers. Distance is in centimeters.

	Movement Preference	
	Day	Night
Preferred tidal cycle	41.62 ± 2.85	45.31 ± 6.17
Non-preferred tidal cycle	14.12 + 5.37	19.42 + 3.46

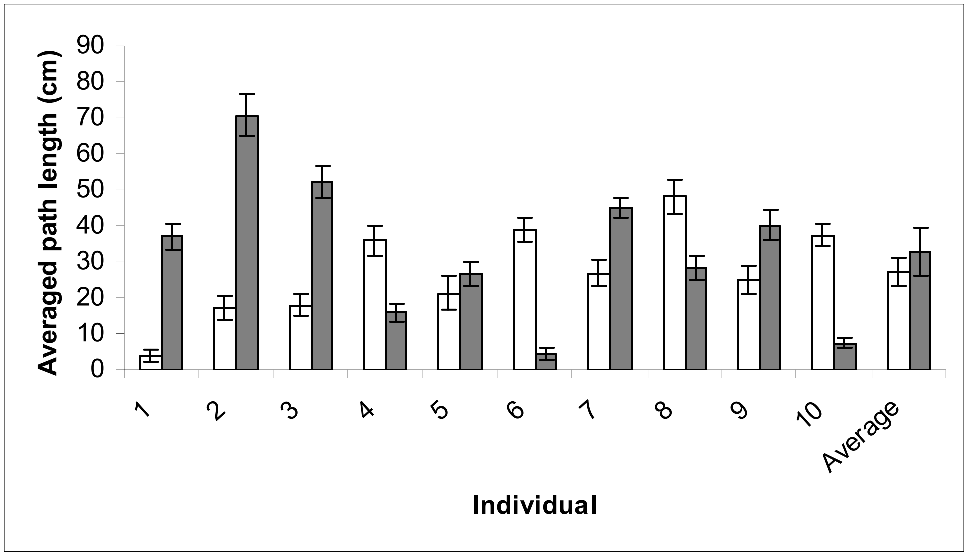


Figure 3.5. The averaged path length for each individual (Error bars are SE, n=10). Individuals moved during both the day (white bars) and night (grey bars). Four individuals moved more during the day high tide while six individuals preferred to move more during the night high tide. Time movement preference did not appear to be related to size. The eleventh column is the combined average for all individuals.

All individuals' foraging increased over the first 9 days. Thereafter, foraging areas continued to increase but more slowly (Figure 3.6). The final foraging area was not significantly related to limpet size (Regression, R^2=0.11, F=.99, n=10, p=0.349). When the three smallest (potentially non-territorial individuals) were removed from the data, the results moved closer to significance (Regression, R^2=0.52, F=5.51, n=10, p=0.066). *Lottia gigantea* is a protandrous limpet, switching from male to female when it reaches a certain size threshold (Wright & Lindberg 1982, Fenberg 2008). Small males are usually non-territorial, while larger females defend their territories against intruders to protect algal resources (Stimson 1970, 1973, Wright 1982). When individuals were compared using the three final foraged areas, ignoring shell length (final area did not depend on shell length) the results were significant (1-way ANOVA, F=10533, n=10, p<0.0001), demonstrating the variation among individuals.

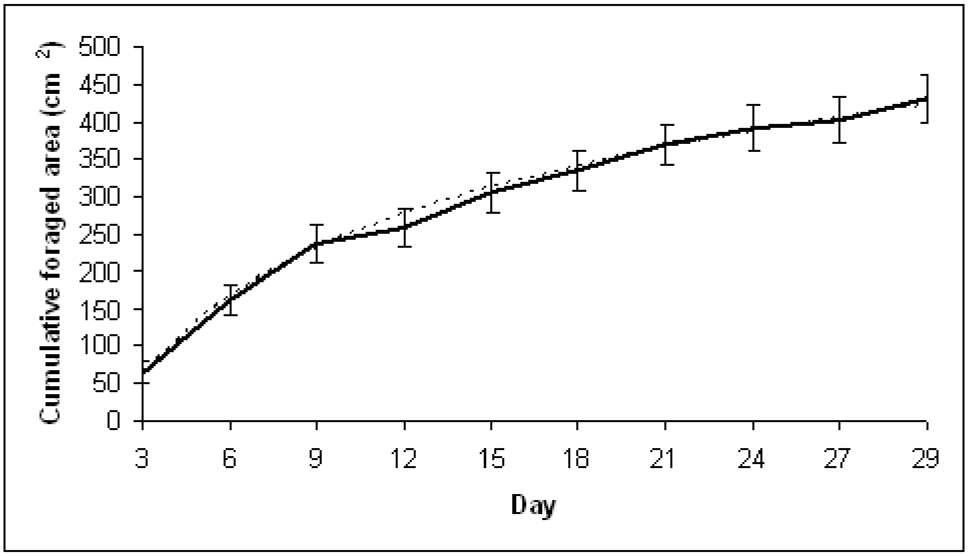


Figure 3.6. Cumulative area foraged for all ten individuals determined from all foraging paths traversed every three days from the start of the experiment. Error bars are SE. The dashed line is the curvilinear trend line (R^2=0.99). The area foraged increased the most over the first 9 days and slowed down for the remaining 3 weeks.

It was hypothesized that territory size would be proportional to path length, but an individual's average path length did not determine its territory size (Regression, R^2=0.28, F=3.13, n=10, p=0.115). The average path length and total area foraged were then scaled to body size and a regression showed that path length/body size was proportional to territory size/body size (Figure 3.7, Regression, R^2=0.44, F=6.21, n=10, p<0.05).

Figure 3.7. Foraged area compared to path length when both were scaled to body length. (Regression, R^2=.44, F=6.21, n=10, p<0.05)

Discussion

The goal of this study was to examine *Lottia gigantea* home range/territory formation. Initially, *L. gigantea* explored large areas of the experimental setup, but displayed location preferences and formed home scars within three weeks. Individuals were not subjected to territorial encounters, therefore all areas of their arenas could be considered to be equally attractive. Individuals returned to familiar areas over the course of four weeks, rather than continuously exploring novel space. The behavior of *L.*

gigantea appears to fit one of the assumptions of the Stamps and Krishnan (1999) model: that an organism will return to areas where it does not experience agonistic encounters and favor familiar areas over novel ones.

The area traversed by *L. gigantea* increased rapidly at the beginning of the experiment, suggesting that the first week of territory establishment may have been an exploratory period. While it could be speculated that individuals were simply hungry at the beginning of the experiment, limpets were kept in holding pens prior to the experiment with more space to traverse (> 1 m^2) than in the experimental setup and a biofilm was always present on the holding pen tiles so individuals had adequate food prior to the start of the experiment. The foraged area increased more rapidly during the first nine days, and thereafter territory expansion began to slow down, but, during the course of the observations, expansion never reached a plateau. During the first nine days the percent increase in cumulative foraged area was > 10% whereas it was < 10% during the last nine days of the experiment. New area was foraged less at the end of the experiment, but individuals could be seen scraping at the edges of their home ranges. Despite the smaller increase in cumulative foraged area at the end of the experiment, individuals moved greater distances during the last nine days. Since the chlorophyll concentrations were lower within the territories at the end of the experiment, individuals may have had to travel longer distances to forage.

In the field, *L. gigantea* shell length is correlated with territory size; larger limpets have larger territories (Stimson 1970). There was no relationship between shell length and territory size in this experiment, but this may have been because not all individuals were territorial. When the daily path length and cumulative foraged area were scaled to shell length, both were inversely related to size; path length determined territory size. In addition, size range may have been too small among the individuals to observe a difference.

Lottia gigantea is a protandrous species, switching from male to female once a certain threshold is reached based on size and territory acquisition (Wright & Lindberg 1982, Lindberg & Wright 1985). Smaller *L. gigantea* are typically male and non-territorial (Wright 1989). If an individual was non-territorial, it would make sense to roam more and forage where there was food. In contrast, larger individuals had a greater affinity to return to home scars than smaller individuals. While all individuals except one demonstrated a homing characteristic, the larger individuals spent a greater amount of time during the active periods on their home scars. Non-homing behavior may be the result of the individual being non-territorial.

The homing behavior of *Lottia gigantea* suggests the species is a central place forager, returning to the same place after each foraging event (Hamilton & Watt 1970, Pyke et al. 1977, Orians & Pearson 1979, Pyke 1984). Other limpets have also demonstrated a central place foraging strategy. Chelazzi (1990) noted that *Patella vulgata*, an eastern Atlantic intertidal limpet species, was a central place forager since it formed a home scar. The formation of a home scar serves not only to reduce desiccation by conforming to the shape of the rock, but also aids in resource accessibility. In the case of *L. gigantea*, returning to a central place ensures that it remains within its defended algal territory.

Foragers can be classified as energy maximizers or time minimizers (Schoener 1969, Hixon 1982). The former maximizes its energy gain to increase its ultimate reproductive success, while the latter minimize its foraging time; a time minimizer receives no further reproductive gain once a certain energy threshold is met. A limpet time budget can be divided into time spent foraging, traveling and resting on its home scar (Evans & Williams 1991). The foraging time budget of *Patella vulgata* has been examined extensively (Wright & Hartnoll 1981, Evans & Williams 1991, Santini & Chelazzi 1996, Chelazzi et al. 1998, Burrows et al. 2000). Through field studies, Evans and Williams (1991) determined that *P. vulgata* was a time minimizer. They hypothesized that *P. vulgata* reduced the amount of time off their home scars to reduce predation and desiccation risks. When Santini and Chelazzi (1996) compared the time budget of *P. vulgata* from field studies to modeled output, they found that *P. vulgata* behaved somewhere between an energy maximizer and a time minimizer. The grazing time was shorter than predicted for an energy maximizer, but longer than that predicted for a time minimizer. They hypothesized that foraging constraints such as a higher energetic need or a slow digestion rate might explain why *P. vulgata* fell in the middle. *Patella vulgata* would appear to be an energy maximizer if it required more food due to reproductive growth but could be classified as a time minimizer if it had to wait for its intake to digest, rather than continuing to forage.

The time budget was not directly analyzed for *L. gigantea*, but based on this experiment, *L.* gigantea may also fall between an energy maximizer and a time minimizer. The foraging time duration would be independent of size if the individual was an energy maximizer (Satini & Chelazzi 1996). Santini and Chelazzi (1996) determined that time minimizers would only graze for one quarter of the foraging period to maintain their necessary energetic intake, but in their study, larger individuals grazed for a longer time proportional to their size. *Lottia gigantea* foraged on both the outbound and return trips during this study. *Lottia gigantea* distinctly swing their heads as they forage, a behavior that is easily observed on the time-lapse videos (pers. obs.). Whenever *L. gigantea* was moving, it was also foraging, which would be indicative of an energy maximizer. In this study, all individuals spent greater than 25% of the active period resting on their home scars. *Lottia gigantea* spent significant amounts of time on their home scars when they could have been foraging (a total of 5.5 hours per foraging cycle). This is a behavior indicative of a time minimizer. Steele (1984) found that individuals spent more time feeding and engaging in encounters with neighbors when they lived in dense populations whereas individuals located in an area with few conspecifics spent more time resting. Steele's results suggest *L. gigantea* may be a time minimizer.

I demonstrated that, under mock intertidal conditions, the owl limpet, *Lottia gigantea*, form home ranges complete with home scars in the absence of competitors or predators. Large individuals formed potential territories more rapidly than small individuals and maintained smaller territories relative to their body size than small limpets. Although most of the home range area was incorporated within the first three weeks, exploration and expansion of the home range continued through the end of the experiment. However, expansion continued at a slower rate. Once home scars were established, large limpets tended to spend less time exploring their potential territories than small limpets.

Bridge II

I focused on establishing a baseline for *Lottia gigantea* home range formation in Chapter III. In Chapter IV, I assess the rate of return to an area with a varying amount of food density. These results led me to another experiment where I tested the tenacity of *L. gigantea* based on the amount of algal biofilm on a tile.

CHAPTER IV

IS THE GRASS GREENER? *LOTTIA GIGANTEA* HOME RANGE FORMATION AT DIFFERENT ALGAL DENSITIES

Introduction

It is assumed that an organism will favor areas with greater food density if few costs are associated with exploiting the resource. An organism feeding in a dense patch of food can alter its time budget and dedicate more to time to other activities, such as mating, since it will spend less time foraging (Hoffman 1983). An animal may reduce the size of its territory if food is abundant, and therefore spend less energy defending its territory (Carpenter 1987). For example, *Lottia gigantea*, the territorial owl limpet, had smaller territories in the field when the algal density was high (Stimson 1973). Limpets are macrophagous generalist grazers, consuming the biofilm found on rocky intertidal substrata (Underwood 1979, Hawkins & Hartnoll 1983). When Stimson (1973) experimentally removed the algal biofilm from the rocks, individuals expanded their territories.

Stamps and Krishnan (1999) proposed a new model of territory formation in which the experience of individuals dictates what locations they repeatedly visit and what locations they avoid. The authors suggest that affiliative experiences increase the likelihood that an animal will return to an area while agonistic experiences at a site will decrease the likelihood of their returning to that site. These assumptions are based on the initial stages of territory establishment when an organism is beginning to explore a novel area. Affiliative experiences could consist simply of a lack of agonistic encounters in a new habitat or an increase in habitat quality such as higher food density.

Optimal foraging theory addresses the costs and benefits an organism experiences while acquiring a food resource (Aronson & Givnish 1983, Pyke 1984). Costs can include searching/handling times, exposure to a potential predator, and energy expenditures. While an animal is foraging, it is exposed not just to predation, but also to the hazards of injury. Berger-Tal et al. (2009) placed nails and razor wire throughout an experimental area to demonstrated that red foxes forage at a slower rate when in a dangerous patch. A slower foraging rate increases the costs of foraging by increasing the time an individual must spend foraging in one patch. Organisms must make decisions, which weigh the risks against the reward, with the ultimate goal of reproductive success.

In the rocky intertidal, wave energy is a significant environmental variable (Judge 1988, Denny & Blanchette 2000, Jenkins & Hartnoll 2001). Waves can dislodge both mobile and sessile organisms from substrata (Denny 1985, 2006). In the case of *Lottia gigantea*, the potential cost of being swept off a rock (death) may affect the decision of whether or not to forage; in other words, the decision to remain still or move. Wright and Nybakken (2007) determined that when wave height exceeded 1 m, *L. gigantea* locomotion was reduced. When exposed to increased drag forces, *L. gigantea* spent less time foraging (Judge 1988). If *L. gigantea* is moving, it is more susceptible to being dislodged by waves, but when stationary, it is difficult to remove *L. gigantea* from the substratum. *Lottia gigantea*, like other homing prosobranch gastropods, has greater tenacity than other gastropods (Davenport 1988, Hahn & Denny 1989). Tenacity is the adhesive strength to the substrate (Davenport 1997). Limpets have higher tenacities when they are stationary than when they are moving (Miller 1974). When exposed to extreme water velocities (25 m/s), there was a 90.7% survivorship of stationary individuals (Denny & Blanchette 2000). Denny and Blanchette (2000) found that it took a tensile force of 190 N to remove a stationary limpet from glass, but only 38 N to remove a moving individual.

The purpose of this study was to determine if *L. gigantea* would preferentially return to areas with abundant food. Because *L. gigantea* is territorial to protect its algal garden, this study tested the assumption that the number of visits would increase to areas with greater habitat quality (higher food density). In contrast to model predictions, individuals actually avoided areas of high algal densities, suggesting that there was a cost associated with these sites. It appeared that *L. gigantea* were physically avoiding the tiles with the highest algal density, but they would graze on the edges of these tiles. To determine if *L. gigantea* were avoiding the high algal areas due to a decrease in tenacity, individuals were plucked off tiles with variable algal density while moving and the force it took to remove them was recorded.

Materials and Methods

Varying Algal Density Experiment

Forty *Lottia gigantea* were collected in May 2008 in Orange, California and shipped overnight to Charleston, Oregon. Ten individuals were selected for this experiment (shell lengths 26.5-45.95 cm). The experiment ran from August 2008-September 2008. *Lottia gigantea* were placed in individual arenas larger than their predicted territory (territories are correlated with limpet size (Stimson 1970)). Arenas were made of unglazed terra cotta tiles placed in a sea table. To keep individuals inside their arenas, a dowel fence was constructed and placed over the tiles and 6 cm long dowels were glued vertically to the shells with epoxy (Figure 4.1). When an individual encountered the fence, the dowel prevented the individual from leaving the arena. To mimic high tide, individuals were splashed with water for 4 hours twice a day, using a dump tank located above the arenas. The dump tank was connected to a flow-through sea water system. Four hours is approximately the amount of time organisms in the splash zone of the rocky intertidal are typically exposed to waves. As in the field, individuals only moved during the high tides (Stimson 1970, Wright & Nybakken 2007). The wave speed was measured by recording the amount of time it took for water to move from the top of the experimental setup to the bottom (0.914 m). The wave speed was 1.2 m/s ± 0.04 (average ± SE, n=20) and waves occurred every 43.8 seconds. The lighting system was a high output fluorescent fixture using four 54 wattage high output fluorescent lights, two yellow and two blue (General Electric, yellow-4700 lumens, 3000 K; blue-4370 lumens, 6500 K). The lights were hung parallel to the setup and the light cycle was similar to light exposure in the field during the fall (12:12 h light:dark).

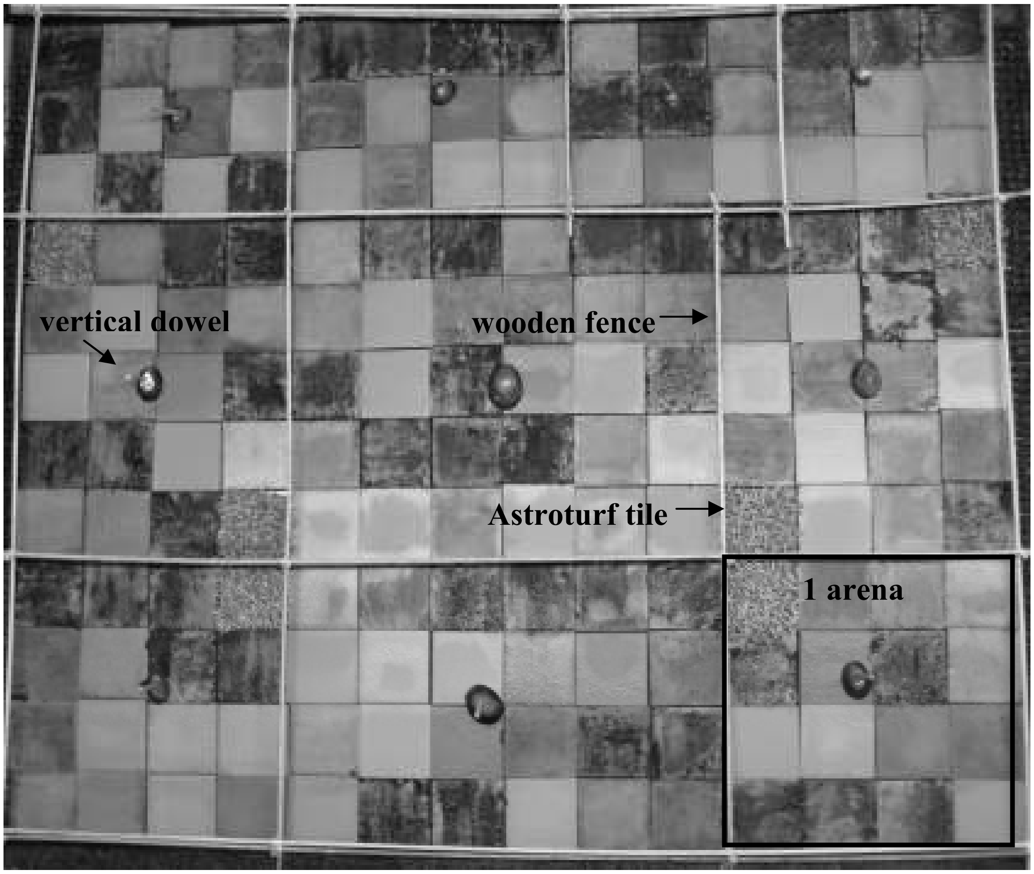


Figure 4.1. Varying algal density experimental setup. Ten arenas with three types of treatment tiles-low, medium and high algal density. Treatment tiles were randomly placed in each arena, based on a multiple of three. Arena size was based on individual size. An arena with 30 tiles received ten tiles of each treatment. If the number of tiles in an arena was not a multiple of three, tiles with Astroturf glued to them were used as space holders. Each arena contained one individual (n=10) and was separated by a wooden fence. Dowels were epoxied vertically to each limpet's shell. When an individual encountered the wooden fence the dowel prevented it from moving into an adjacent arena. Each tile side=7.6 cm

Lottia gigantea are microphagous generalist grazers and their diet consists of the algal biofilm found in the rocky intertidal. Prior to the introduction of *L. gigantea*, the tiles were seeded from unfiltered sea water via the dump tank flow-through watering system. Thus, the biofilm growing on the tiles was their food source. The three treatments used were low, medium and high algal cover on the terra cotta tiles. The chlorophyll concentrations for the three treatments were 0.004 ± 0.003 μg/cm^2 (low), 0.857 ± 0.318 µg/cm^2 (medium), and 6.203 ± 1.369 µg/cm^2 (high) (mean ± SE). Chlorophyll densities in the rocky intertidal range from 0.01 to 40 µg/cm^2 (Nicotri 1977, Gray & Hodgson 1998, Jenkins et al. 2001, Boaventura et al. 2003, Kido & Murray 2003, Morelissen & Harley 2007, Underwood & Murphy 2008).

Tiles with low algal density were placed on the setup one week prior and scrubbed with a scouring pad two days before the start of the experiment. Medium algal density tiles were placed on the setup three weeks prior to the start of the experiment. Medium tiles had a visible uniform coating of diatoms and blue green algae. High algal density tiles were placed on the experimental setup six weeks prior to the start of the experiment to ensure maximum algal growth prior to the start of the experiment. High algal cover tiles were covered with a thick algal carpet, consisting of filamentous green algae and macroalgal propagules. Chlorophyll samples were randomly taken from low, medium and high tiles before and after the experiment using the standard chlorophyll extraction technique to confirm the visual algal estimate (Parsons et al. 1993). Fifteen samples were randomly taken from the experimental setup (5 from each treatment). Samples were scraped from the tiles and extracted using ethanol and measured in a fluorometer (TD-700 Laboratory Fluorometer, Turner Designs).

Each arena contained randomly placed tiles of the three algal densities. Equal numbers of tiles were used for each algal density. The total number of tiles was based on a multiple of three to ensure that there was proportionally the same amount of food per arena. If the number of tiles in the arena was not a multiple of three, tiles with Astroturf epoxied to them were placed in the arena. These tiles served as spaceholders. *Lottia gigantea* will not cross Astroturf so the spaceholders were placed in corners of the arena.

If an individual had twenty tiles in its arena, two Astroturfed tiles were inserted. The size of the arena was based on the size of the individual, as *L. gigantea* territory size has been correlated with limpet length (Stimson 1970).

The individuals were placed in the middle of their respective arenas and photographed for four weeks using a Nikon Coolpix 5700 camera connected to a Digisnap time-lapse controller (Harbortronics, Inc. Model 2100). During the simulated high tide, a picture was taken every 15 seconds for 5.5 hours. Pictures were only taken during the high tides as individuals did not move when the tiles were not wet (Stimson 1970, pers. obs.). Although high tide was only 4 hours, an additional 1.5 hours of additional photographing after the end of the high tide were taken to ensure all movement was recorded. *Lottia gigantea* does not move when it is not splashed by waves, but it will continue to move when the substratum is wet (Stimson 1970, Wright & Shanks 1993, personal observation).

An organism was considered to be homing if it returned to the same location (home scar) after each foraging event (Wells 1917, Underwood 1979, Chelazzi 1990). Typically, *L. gigantea* only moves when being splashed by water and doesn't begin moving until twenty minutes after first being wetted (Stimson 1970). The limpets were filmed for 11 hours each day and were only splashed with water for 8 hours. The first twenty minutes and last 1.5 hours of each filming session accounted for 33% of the footage. Individuals were considered homing if they spent 33% of their active time in the same spot, meaning they were returning to a home scar during each foraging event. As the home scar data were processed, it was determined that some individuals preferred up to three locations, so the home scar definition was expanded to include three spots.

The time-lapse pictures were converted to video using MakeAVI software (http://sourceforge.net/projects/makeavi/), converted to Quicktime videos using AVS Video Converter (version 6.2) and analyzed with NIH ImageJ software. A grid that divided the tiles into quarters was placed over the computer screen and the position of each individual was scored every 10 frames for 1320 frames, for each video (84 videos total). An individual was considered in a grid square if greater than 50% of its body was in the grid. Each visit to a grid (every 10 frames) was scored was scored with a '1.' If a limpet's shell was between two grids or one fourth in four grids, the visit was divided into .5 or .25 for each of the grids. Movements were scored to examine the probability of return based on the amount of biofilm present. The time spent on each treatment tile (low, medium and high algal density) was summed for the entire experiment to determine where individuals spent the most time during their active periods. To visualize where individuals were moving, daily path lengths of the foraging limpets were traced on a piece of acetate placed over the computer screen. Path length data were not quantified.

Foraging behavior under conditions of varying algal density was analyzed by summing the number of visits to each treatment tile of low, medium and high algal density. The data were first converted to a percent of the total number of visits, then arcsine transformed, and analyzed using one-way ANOVA (Systat version 11).

Tenacity Experiment

After analyzing the responses to different algal densities, I hypothesized that individuals avoid tiles with high algal density due to a loss of suction. To test the tenacity of *Lottia gigantea*, individuals were plucked from tiles with different algal densities in August 2010. Three algal treatments were used: tiles with low, medium and high algal density, and densities were similar to those used in the grazing experiment in 2008. Twenty-seven individuals were used, nine per algal density. Individuals were placed on separate treatment tiles and allowed to acclimate for two hours prior to the beginning of the tidal cycle. Individuals acclimated for no more than two hours to ensure that limpets were using adhesion rather than glue to stick to the tiles. *Lottia gigantea* has been shown to produce a glue when it remains on the same substratum for < 12 hours (Smith 1991, 1992, 1993). The tiles were placed in a frame that allowed the limpets to be plucked without the tiles moving. The high-tide simulation began after 2 hours of acclimation and the individuals were plucked twenty minutes after the high tide began. Individuals were removed by attaching a spring scale (Pesola brand, 5 kg maximum) to a string tied to a ring, attached by epoxy to the limpet's shell. Individuals were plucked while moving to mimic feeding behavior, as in the prior experiment. In the algal density experiment, individuals foraged around their arenas, usually avoiding dense algal tiles. Individuals were pulled at a consistent rate, perpendicular to the tile. The force required to pull the individual off the tile was measured in kilograms and converted to Newtons. To determine whether or not limpet size (shell length) affected the force required to remove a limpet from a tile, size and force were analyzed with linear regression for each treatment tile (Table 4.1). A one-way ANOVA with planned comparisons was used to look at the tile treatment compared to the force necessary to remove a limpet (SAS version 9.1).

Table 4.1. Tenacity experiment. Linear regressions were used to show that there was no significant relationship between individual size and the force it took to pluck an individual from a tile. Three treatments were used: tiles with low algal density, medium and high.

Algal Density	F	p	R^2
Low	4.86	0.06	0.41
Medium	0.01	0.92	0.00
High	2.84	0.14	0.289

Results

The amount of biofilm was within the range found naturally occurring in the rocky intertidal (Table 4.2). The chlorophyll concentrations within each treatment did not differ significantly between the beginning and end of the experiment for any of the treatments (one-way ANOVA, n=5 (per treatment); low F=3.25, p=0.11; medium F=3.08, p=0.11; high F=0.78, p=0.40). By the end of the experiment, the density of chlorophyll stayed the same or decreased for the low and medium algal density tiles, respectively, while the chlorophyll density on high algal density tiles increased. Although the results were not statistically significant, the density differences suggest that the low and medium algal density tiles were being grazed while the high algal density tiles were not.

Table 4.2. Varying algal density experiment. Chlorophyll samples were taken before and after the experiment (before n=15 (5 per treatment) and after n=15 (5 per treatment)) Values are reported as mean ± SE.

Algal Density	Before	After
Low	0.004 ± 0.003 μg/cm^2	0.006 ± 0.002 μg/cm^2
Medium	0.857 ± 0.318 μg/cm^2	0.250 ± 0.136 μg/cm^2
High	6.203 ± 1.369 μg/cm^2	9.168 ± 3.057 μg/cm

Individuals were followed for four weeks using time-lapse photography. The total number of visits to each treatment tile was compiled to determine which algal density treatments individuals spent their time. Six individuals formed home scars within two weeks, returning to one or two locations after each tidal cycle. By the end of four weeks, nine individuals returned to home scars while one individual showed a preference for two locations, spending 20% of its potential active time (i.e., when splashed or wet) at these two spots. Although home scar formation was not examined in-depth for this experiment, the establishment of a home scar and home range demonstrates that individuals were behaving normally in the laboratory. After four weeks, home range size was correlated with limpet size (Figure 4.2). Larger individuals formed larger home ranges.

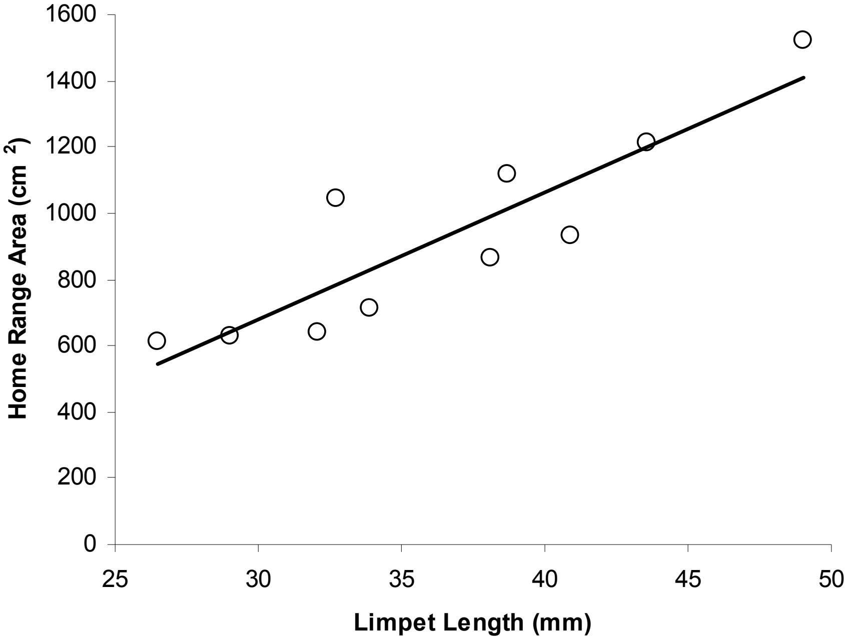


Figure 4.2. Limpet size (shell length) vs. home range size. A significant positive linear relationship was found between limpet shell length and home range size (Regression, R^2=0.79 F=30.39, n=10, p=0.001).

The number of visits to the different treatment tiles was summed for each individual. The percent of visits differed significantly among low, medium, and high algal density tiles (one-way ANOVA, n=30, F=12.23, p<0.0001). Visits to the high algal density tiles were significantly fewer than to the low and medium density tiles (Figure 4.3, Tukey's HDS, p=0.007). Individuals spent the majority of their foraging time on low or medium dense tiles (Figure 4.3). There was no significant difference between time spent on low and medium algal density tiles (Tukey's HDS, p=0.314). When the individual foraging paths were overlaid with a picture of the experimental setup, it was clear that individuals avoided the high algal density tiles and the Astroturf tiles (Figure 4.4).

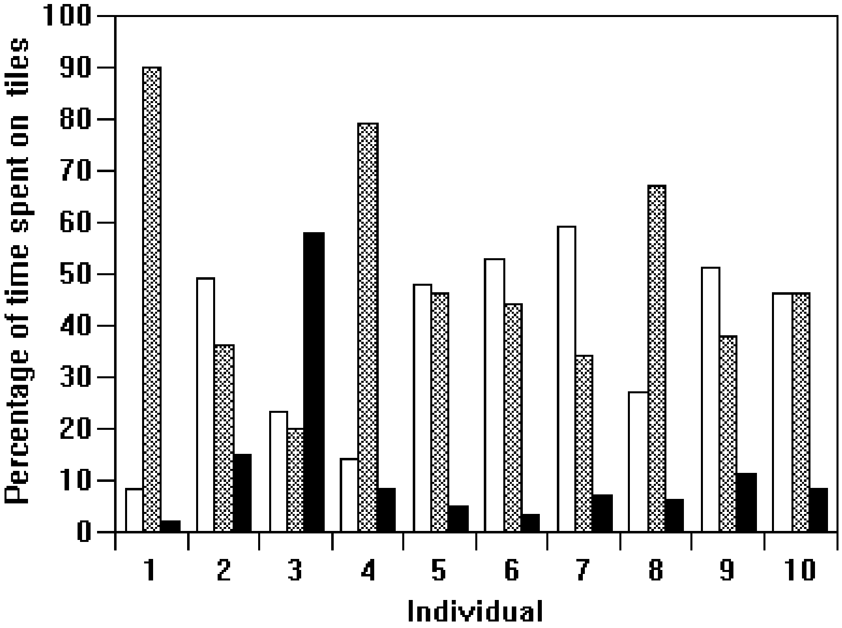


Figure 4.3. Percent of total observation time individuals spent on each of the three tiles with different algae densities (low density-white bars, medium density-hatched bars, high density-black bars). The percentage of time spent on low and medium algal tiles was not significantly different, whereas significantly less time was spent on the high algal density tiles (one-way ANOVA, n=10, F= 12.23, p<0.05).

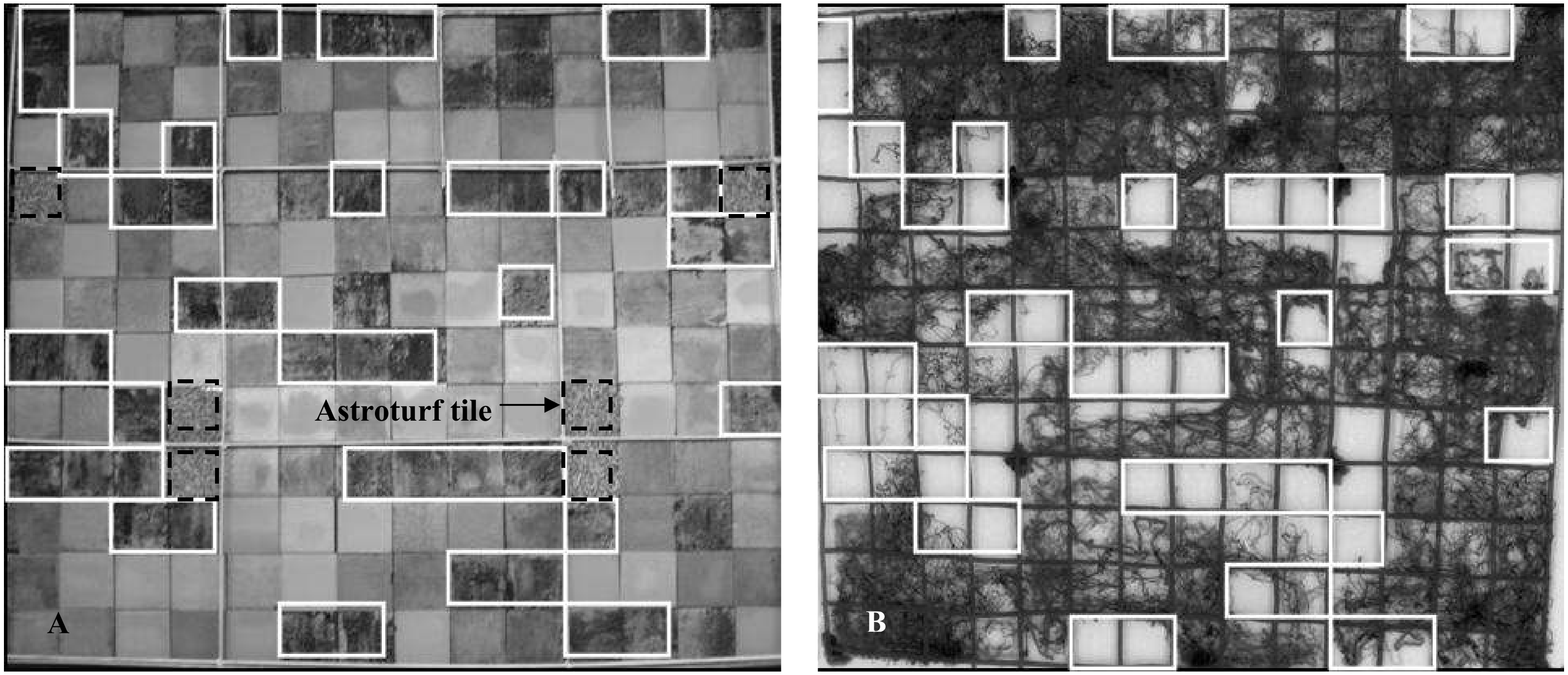


Figure 4.4. Varying algal density experiment. A. Experimental setup. B. Tracings of the individuals' paths over the course of 60 days. The outlined white boxes in both pictures were tiles typically avoided by individuals, i.e. algal dense tiles. The tiles surrounded by dashed black lines in A. were Astroturf tiles placed in the corners so each arena contained a multiple of three.

To examine the role of algal density and limpet tenacity, individuals were plucked from tiles with varying algal density. Limpet size did not affect the force required to remove a limpet from the substrate and limpet size was eliminated as a factor and one-way ANOVA was used to examine differences among the three algal treatments (SAS version 9.1). Normally it takes greater force to remove larger limpets (Wright, unpublished data), but the size range (< 10 mm) was small enough that it did not influence the force needed to remove an individual.

The chlorophyll concentration for the three treatment tiles was comparable to those in the field. In the experiment, low algal dense tiles had an average ($\mu g/cm^2 \pm$ SE) of 0.00 ± 0.00 $\mu g/cm^2$, medium algal dense tiles had 0.28 ± 0.04 $\mu g/cm^2$, and the high algal dense tiles had 1.82 ± 0.16 $\mu g/cm^2$. Limpets placed on tiles with high algal density were easily pulled off; it took a force of 2.62 ± 1.20 N to pull an individual off a tile with high algal density while the force needed to pull a limpet off the tiles with low and medium algal densities was 22.72 ± 4.17 N and 25.72 ± 3.67 N, respectively. There was a significant difference in the force needed to pull a limpet off a tile among the low, medium and high treatments (one-way ANOVA, $F=14.65$, $n=27$, $p<0.0001$). In the tenacity experiments, significantly less force was required to pull a limpet off a high algal density tile than from a tile with a medium or low algae density (Figure 4.5, planned comparison, high vs. low + medium, $p<0.0001$). There was no significant difference in the force required to remove a limpet from the medium and low algal density tiles (Tukey's HDS, $p=0.8$).

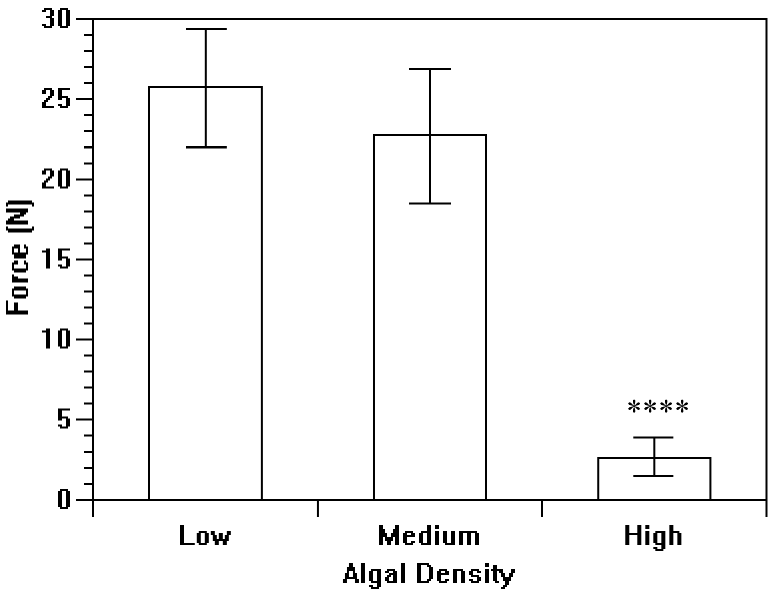


Figure 4.5. Average amount of force (Error bars are SE) required to remove a moving limpet from a tile, based on the amount of algae present, varying from minimal (low treatment) to high algal density. The force necessary to pull an individual off a tile was significantly lower on the high algal density tiles (one-way ANOVA, n=9 per treatment (27 total), planned orthogonal comparison, $p<0.0001$).

Discussion

The Stamps & Krishnan model (1999) predicts that an individual is more likely to return to an area where it had positive experiences. The territories of *Lottia gigantea* are visible algal films in the rocky intertidal and *L. gigantea* display territorial behavior to protect their food sources (Stimson 1970). When Stimson (1973) experimentally reduced the amount of algae in *L. gigantea* territories, individuals expanded their territory sizes. To explore the possibility that an individual would return more frequently to an area with a greater food resource, *L. gigantea* were exposed to varyious amounts of food in individual arenas. It was assumed that limpets would prefer tiles with greater food density.

In the varying algal density experiment, *L. gigantea* avoided traveling on tiles with a thick algal covering. While it is possible that *L. gigantea* have an algal species preference, this is unlikely as individuals grazed on the edges of high algal density tiles, but avoided moving onto or traversing them. This suggests that avoidance was not due primarily to food preferences and that the algal-covered substrate was associated with costly risks. Limpets ingest macroalgal propagules and when limpets are experimentally removed from an area, the macroalgae that grows in the absence of grazers becomes too large for the micrograzers to feed on; the limpets are outcompeted by the algae (Hawkins & Hartnoll 1983). *Lottia gigantea* are microphagous generalist grazers and while they consume macroalgal propagules, the ephemeral algae growing on the tiles in the varying algal density experiment may have escaped herbivory via a large prey refuge (Molles 2001). Sizable prey is difficult for a predator to physically handle. The algae present on the highest density tiles may have been physically too large for *L. gigantea* to consume. Although *L. gigantea* avoided high algal density tiles, there was no difference between the number of visits to the medium algal and low algal density treatment tiles, indicating that individuals did not prefer one of these treatments over the other. While the low algal density tiles had a minimal amount of biofilm on them, it may have been enough to sustain individuals, or the four week experiment wasn't long enough to starve them. In addition, the mucus of *L. gigantea* has been shown to promote algal growth (Connor & Quinn 1984, Connor 1986). *Lottia gigantea* may have been able to cultivate a biofilm on tiles with little algae.

One potential explanation may be that the algal mat was simply too slippery and that limpets avoided the possibility of losing grip by not moving onto tiles with a thick biofilm. The avoidance suggests there is a possible trade-off between an abundant food and the risk of becoming dislodged from the substrate. Limpets were removed from high algal density tiles with significantly less force than required to remove an individual from medium or low algal density tiles. Denny and Blanchette (2000) calculated that a force of 190 N was required to removed a 5 cm long limpet while it was stationary, but only 38 N was required when it was crawling. These results are similar to the dislodgement force found to remove a limpet from the low or medium algal treatments in this study (24.2 ± 2.7 N). In addition, all limpets were < 5 cm long in this study.

The costs of potential death due to dislodgement may outweigh the benefits of a large food source. When individuals were removed in the tenacity study, their entire foot was covered in algae as they could not grip the tiles. *Lottia gigantea* has been shown to cease movement when wave height reaches a certain threshold (> 1 m) (Wright & Nybakken 2007). In addition to foraging, *L. gigantea* is territorial and spends time defending its territory against intruders. It was determined that individuals engaging in a territorial interaction (both intruders and territory holders) were much easier to pluck off a rock than other moving limpets and limpet tenacity decreased with increasing speed (Wright, unpublished data). Thus, is a trade-off between the benefit of defending a food source and the cost of being swept off the rock.

The importance of limpets as microphagous grazers has been examined in terms of both foraging (Della Santina et al. 1995, Chelazzi et al. 1998a, Chelazzi et al. 1998b, Burrows et al. 2000, Jenkins & Hartnoll 2001) and the effect of grazing on algal succession ((Castenholz 1961, Lindberg 1986, Kim 1997, Lindberg et al. 1998). Large grazer foraging patterns can have an effect on the rocky intertidal structure, altering both the floral and faunal landscape. *Lottia gigantea* bulldozes intruders out of its territory, even sessile barnacles (Stimson 1970). Nicotri (1977) found that three species of *Lottia* dramatically altered the algal composition and reduced the amount of biofilm found on the substrate by grazing on diatoms. Diatoms with greater adhesive strength remained on the rock while other diatoms were scraped off the rock. In the intertidal, food is rarely equally distributed in an area. Patchiness in both algal density and limpet grazing can also play a role in intertidal zonation (Johnson et al. 1997, Jenkins et al. 2001, Johnson et al. 2008). Johnson et al. (1997, 2008) found that over time, algal patchiness caused by limpet grazing did not average out. They attributed this to the inconsistency to limpet grazing patterns and irregular topography. *Lottia gigantea* appears to prudently graze the biofilm inhibiting algal colonization by ‘gardening’ which cultivates a biofilm that promotes the growth of ephemeral algae (Branch 1992). It appears that while *L. gigantea* can play a significant role in determining rocky intertidal biological terrain, the biological terrain can also determine *L. gigantea* foraging movement, once the macroalgae reaches a critical size and can escape grazing. Limpets can graze within a patch as long as the algae are at a low density, but once the algal biofilm surpasses a certain threshold, limpets may avoid the area due to a loss of tenacity. While limpets grazed on the edges of tiles with high algal density, they did not crawl on it. Algae escaped predation by creating a slippery surface.

Bridge III

By varying the amounts of algal biofilm it was shown that *Lottia gigantea* actually avoided areas with the greatest amount food in Chapter IV. I determined that it may avoid tiles with high algal density due to a loss of adhesion to the tile. In Chapter V, I began to examine how individuals establish territories.

CHAPTER V

FIGHT OR FLIGHT: *LOTTIA GIGANTEA* TERRITORIAL INTERACTIONS

Introduction

Intertidal invertebrates live in a crowded world bordered by extreme physical forces. Despite their apparent immobility during low tides, many of these animals lead active lives during high tide when conditions are favorable. These active lives may include territorial defense of a mate or a territory (Connell 1963, Knowlton & Keller 1982, Wada 1993, Iwasaki 1995, Baeza et al. 2002, Baeza & Thiel 2003). The territorial owl limpet, *Lottia gigantea*, protects food resources by behaving aggressively toward other limpets that enter their territories (Stimson 1970, 1973, Wright 1982, Wright & Shanks 1993, Shanks 2002). Aggressive behaviors include using its shell to dislodge an intruder or pursuing an intruder to the periphery of its territory.

Despite the historical interest in territoriality, the how and why of territory establishment is largely unexplored. Most studies have looked at what organisms do once a territory has been established. Game theory has been the archetype model to explain territoriality, but recent models suggest that the paradigm may be shifting. When organisms encounter new space, it was thought that the strongest competitor would win, based on the assumption that they possessed greater strength, endurance or already held territory. While game theory provided the foundation for studying territoriality, it is applicable in limited situations due to its focus on unilateral decisions, rather than on whole interactions. In addition, game theory does not address how territories are formed. Stamps and Krishnan (1999, 2001) presented an alternative model to explain territory establishment, one based on a progression of learned behavior. Territory acquisition may be based more on the persistence of the competitors, that is, whether or not they consistently return to an area. When newcomers arrive at a site, their decisions to occupy the site or leave may be based on the affiliative or agonistic experiences they have at that area; affiliative experiences, such as visiting an unoccupied area, may lead to territory formation whereas agonistic interactions, such as fighting, may cause them to leave. Individuals, therefore, learn which spaces to avoid and which to defend as exclusive space. If an individual does not experience any agnostic encounters as it investigates a novel space, it is more likely to return to these areas in the future and incorporate them into its territory.

Territorial models present a simplified version of territorial interactions such as how territories are established or what happens when a resident encounters a newcomer in its territory yet they require several assumptions to be met. For example, the Stamps and Krishnan (1999) territorial acquisition model is based on four assumptions: 1) the organisms are mobile, 2) the habitat is spatially heterogeneous, 3) the habitat features are stable, and 4) the area is large enough to support multiple contiguous territories. The Stamps and Krishnan models have been tested a few times, but only with vertebrates (Stamps & Krishnan 2001, Bruinzeel & van de Pol 2004). Animal behavior research often focuses on vertebrates, but vertebrates generally occupy relatively large territories making experimentation difficult. *Lottia gigantea* meets all the conditions designated by the Stamps and Krishnan models and can be tested in a laboratory setting, using multiple animals.

Stamps and Krishnan assume an individual will not return to an area where it experiences an agonistic experience. To determine the probability of return based on agonistic experiences, a pair of limpets were placed in a novel area and monitored for interactions. The goal of this study was to examine the interactions of equal-sized *L. gigantea* as they established home ranges and potential territories. For six weeks, I classified the types of behaviors exhibited by each individual in the event of a confrontation, their level of aggression toward conspecifics and the use of areas in which confrontations occurred.

Materials and Methods

Limpets were collected in Orange, California and shipped to Charleston, Oregon in May 2008. Individuals were placed on unglazed terra cotta tiles on a sloped platform. Unglazed terra cotta tiles, when coupled with a flow through seawater system, promote biofilm growth and ensure a healthy food supply for *Lottia gigantea.* Limpets are microphagous grazers and will eat bacteria, diatoms and macroalgae propagules that grow on tiles in the lab (Underwood 1979, Hawkins & Hartnoll 1983). To mimic waves, a dump tank was placed above the platform. The tank filled with water, tipped over, then righted itself due to a counterweight system. The individuals only moved during the high tides when the dump tank was on, which occurred every twelve hours, for four hours. The lights were on a 12:12 light:dark cycle, similar to the natural light cycle in spring. For complete *L. gigantea* husbandry, see Chapter II.

The experiment began in October 2008. Fourteen individuals were used and two individuals were placed in each of seven arenas (Figure 5.1). To keep individuals contained in an arena, a wooden fence was placed over the tiles and a wooden dowel was vertically attached with epoxy to the shell of each individual. When an individual encountered the fence, the dowel prevented the individual from moving into the adjacent arena (Figure 5.2). Individuals ranged from 26.9 - 45.2 mm and limpets of comparable size were used for each dyad. The difference in size between individuals in a dyad was ≤ 2 mm.

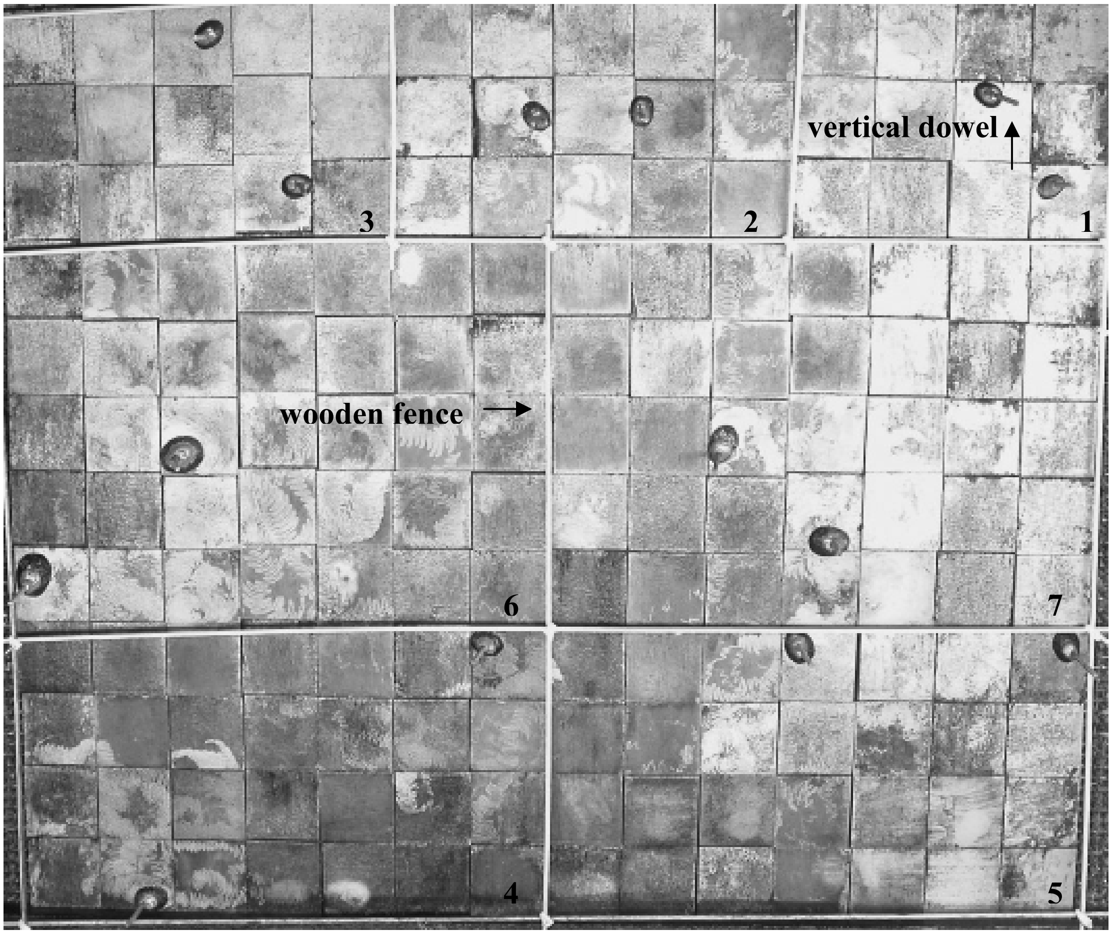


Figure 5.1. Experimental setup. Vertically oriented dowels were glued to each individual's shell with epoxy. When an individual encountered the wooden fence, the dowel prevented it from leaving its arena. The wooden fence was used to create seven arenas. Each arena contained two similar-sized individuals (≤ 2 mm difference in shell length), a dyad. The substrate was unglazed terra cotta covered with an algal biofilm which served as the food source. The dyads were numbered 1-7 (number located in the lower right corner of each arena). Each tile side = 7.6 cm

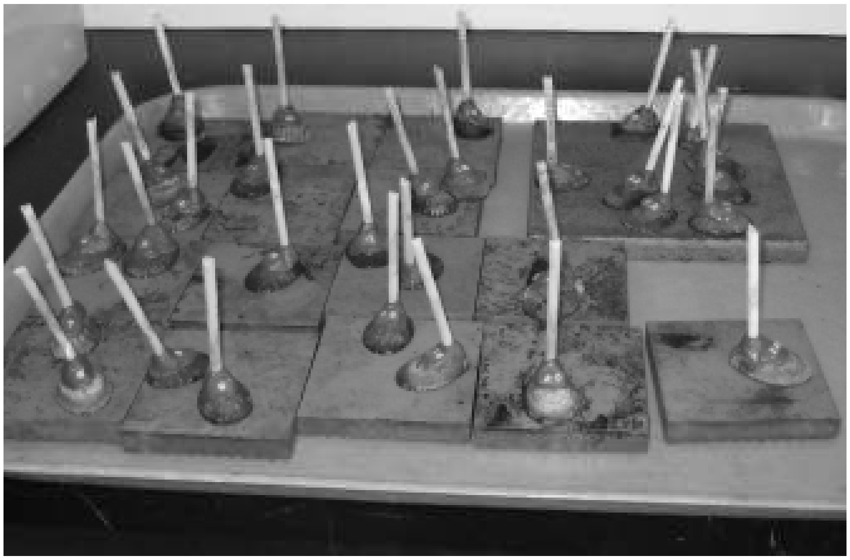


Figure 5.2. Limpets with attached dowels. Z-Spar splash zone epoxy was used to attach 6 cm dowels to each individual's shell.

Arena size was determined by calculating the needed area for each individual to form a territory and reducing it by 20% and then doubling the size for the two individuals. The size of the territory was based on field studies by Stimson (1970) who found that territory size was correlated with limpet length. Individuals were placed in arenas large enough to form territories, yet small enough to force interactions to occur. At the beginning of the experiment, individuals were placed in the middle thirds of the arena, with no divider between them.

Individuals were photographed for six weeks using a Digisnap time lapse controller (Harbortronics, Inc. Model 2100) attached to a Nikon Coolpix 5700 digital camera which was mounted above the setup. During the high tide, a picture was taken every 15 seconds, for 5.5 hours. High tide ran for four hours, but the camera took pictures an additional 1.5 hours after the tide ended to ensure all movement was recorded. *Lottia gigantea* does not move when not being splashed by water, but some moved right after the water ceased and the tiles were still wet. The pictures were converted to video using MakeAVI software (http://sourceforge.net/projects/makeavi/) and then converted to Quicktime videos using AVS Video Converter 6.2) and analyzed with NIH ImageJ software. A grid was placed over the video and the position of each individual was scored every 10 frames, for 1320 frames, for 85 videos.

One of three behaviors (territorial, evasive or no reaction) was recorded for each individual when it encountered its dyadic neighbor. In the field, a territorial *L. gigantea* shoves its shell against the intruder. If the intruder is not knocked off the substrate, the territory holder then chases it to its territory boundary (Stimson 1970). When an individual is evasive and encounters another limpet, it turns > 90º away from the other individual and quickly retreats from the area (Wright 1982). These behaviors were displayed in the laboratory. An individual was considered territorial if it demonstrated territorial behavior in more than half of its interactions with its dyadic neighbor. An individual was considered evasive if it quickly retreated for half or more of its interactions even if it showed territorial behavior. Only interactions where an individual was territorial or evasive were considered when determining overall individual behavior. A 'no reaction' reaction occurred when an individual bumped into its dyadic neighbor and continued moving at the same speed and in the same direction as prior to the encounter.

Every interaction was recorded for each dyad. Encounters where individuals from different dyads interacted at arena boundaries (i.e., at the fence) were noted, but not used in the analysis. Each interaction was classified into one of six categories, based on the reaction of each individual. The six categories were: evasive/evasive, evasive/no reaction, territorial/evasive, territorial/no reaction, territorial/territorial and no reaction/no reaction. The duration of the interactions was recorded and the location of each individual where the interaction occurred was documented. The number of visits to the encounter location was calculated for one week before the encounter (including the number of visits during interactions) and one week after; for days at the beginning and end of the experiment, the possible number of days before and after an encounter was used. One week was sufficient time for an individual to return to an area. The percent change between the number of visits prior to the encounter and after was calculated. If the change was >10%, it was scored as an increase or decrease in the number of visits to the agonistic location. The number of increases, decreases or no change was then compared with the reaction (territorial, evasive or no reaction) of the individual. One dyad only had one interaction and the two individuals were not included in the statistical analysis (dyad #4). Individuals were placed in two groups based on their overall behavior-territorial or evasive based on the criteria listed above. To test for independence a G-test was used to compare the total number of increases and decreases within each group and then these were compared between the two groups (SAS version 9.2).

Results

Twelve of the 14 individuals formed home scars by the end of the second week. All but one individual formed a home scar by the end of six weeks. Limpets are considered homing if they return to the same location (home scar) after each foraging cycle (Chelazzi 1990). A homing limpet will spend the majority of its time on its home scar when it is not foraging. Having a home scar prevents desiccation and makes a limpet less susceptible to predation since its shell conforms to the rock, making it difficult to remove (Hahn & Denny 1989).

Individuals were categorized as territorial or evasive. Three individuals were territorial and 9 were evasive. All three territorial individuals displayed territorial behavior in 75% or more of their encounters (Table 5.1). The evasive individuals varied in their degree of evasiveness. With the exception of the dyad with one encounter, all evasive individuals showed territorial behavior in at least two interactions (Figure 5.3). Three individuals were territorial in half of their interactions and evasive in the remainder. One individual displayed evasive behavior 57% of the time while five individuals were evasive 80% of the time.

Table 5.1. The number of interactions per dyad. Reactions were classified as territorial, evasive or no reaction.

Dyad	# of Interactions	Individual	Territorial	Evasive	No Reaction
1	31	1	18	4	9
		2	5	19	7
2	32	3	9	9	14
		4	3	19	10
3	29	5	4	16	9
		6	9	9	11
4	1	7	-	-	1
		8	-	1	-
5	11	9	5	5	1
		10	3	4	4
6	32	11	18	0	14
		12	2	15	15
7	25	13	12	4	9
		14	3	12	10

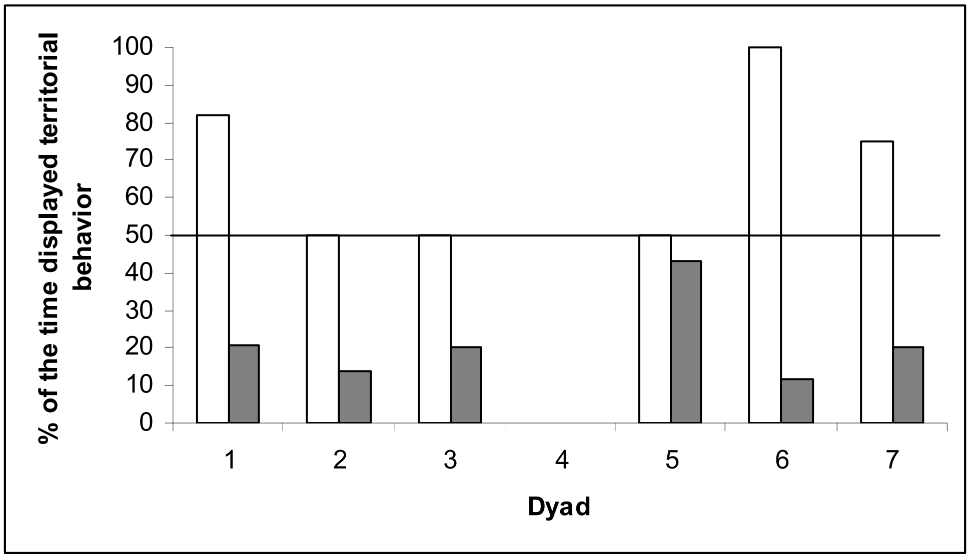


Figure 5.3. The percent of the time an individual displayed territorial behavior based on the total number of interactions per dyad (n=14 individuals, 2 per dyad). The total number of interactions for each individual was based on when it displayed territorial or evasive behavior. Encounters where the individual had no reaction to the interaction were not considered. Individuals that displayed territorial behavior > 50% of the time were considered territorial (individuals in dyads 1, 6 and 7, n=3) and individuals that were territorial ≤ 50% were classified as evasive (remaining individuals, n=11). The individuals in dyad four only had one interaction and neither individual was territorial.

Most dyads had many encounters, ranging from 11 to 32 over the six week period with an average of 23 interactions (Figure 5.4). Only one dyad had just one encounter (dyad #4). There was <25% exclusive area for individuals in each dyad, except for the dyad with only one encounter. These two individuals each had 85% exclusive area; their territories were nearly isolated from each other, limiting interactions. There were 161 interactions among the dyads. Out of the 161 interactions, 103 lasted less than one minute. Longer interactions occurred when one individual displayed territorial behavior and shoved while the other individual clamped down onto the substrate and did not move. The interactions were placed in six categories based on the two individuals' behaviors (Table 5.2). The two most common interactions were evasive/no reaction and territorial/evasive.

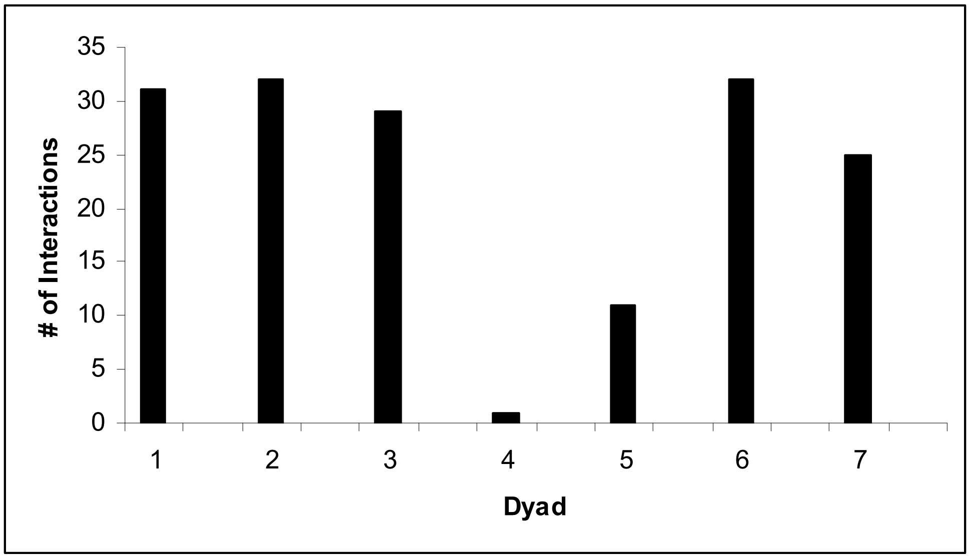


Figure 5.4. The total number of interactions per dyad during the six week experiment. Dyad #4 had only one interaction and was not used in the statistical analysis.

Table 5.2. The type of interaction between individuals in each dyad. Interactions were classified based on the reaction of each individual. Three behaviors were recorded- evasive (Evas), no reaction (NR) and territorial (Terr).

	Interaction						
Dyad	Evas/Evas	Evas/NR	Terr/Evas	Terr/NR	Terr/Terr	NR/NR	Total
1	-	9	14	7	1	-	31
2	2	15	9	3	-	3	32
3	2	13	8	5	-	1	29
4	-	1	-	-	-	-	1
5	1	3	4	2	1	-	11
6	-	8	8	12	-	4	32
7	1	5	9	4	1	5	25
Total	6	54	52	33	3	13	161

When the location of each interaction for each dyad was mapped out, the encounter sites were distributed throughout each individual's home range. The location of each interaction was haphazard and simply occurred when the two individuals encountered one another. The number of encounters that occurred in the middle of the home ranges was compared to the number of encounters at the boundaries and there was a trend; more interactions occurred in the middle that at home range peripheries

(Unpaired t-test, n=10, p=0.07). No pattern emerged when the interactions were looked at sequentially meaning an individual would vary its behavior switching from evasive to territorial or territorial to evasive.

When the number of visits before and after an encounter was compared with the overall behavior of each individual, territorial individuals either returned or avoided the area with the same frequency (Figure 5.5). The difference between the number of increases and decreases in visits to an interaction site were compared within the territorial individuals and the territorial individuals did not vary in their behaviors (G test for independence, n=3, p=0.77). All three individuals increased or decreased their visits to interaction locations at the same rate. Individuals that were predominately evasive avoided areas where they had an interaction, regardless of their behavior (territorial, evasive or no reaction) during the interaction. Evasive individuals were compared based on whether or not they returned to an encounter location. The difference between the amount individuals increased or decreased visits varied, but all decreased visits to areas where they encountered dyadic neighbors. When the number of decreased visits was compared to the total number of interactions for each dyad, all evasive individuals decreased the number of visits by 58% or more (average 75.93% ± 3.81). The variance was potentially caused by the degree of evasiveness each individual displayed (G-test for independence, n=11, p<0.001). The three least evasive individuals, i.e., the potentially territorial ones, did not differ in behavior when the number of increased visits was compared to the number of decreased visits (G-test for independence, n=3, p=0.14).

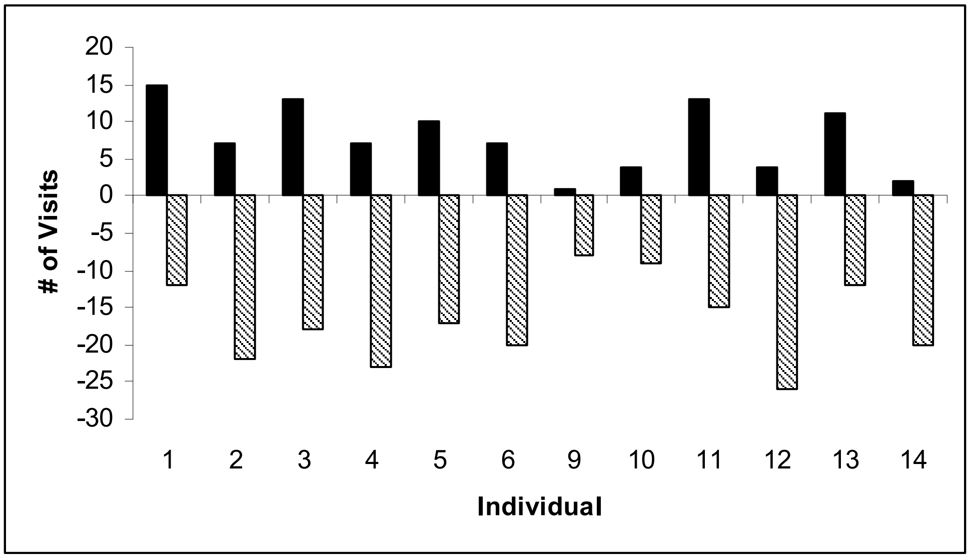


Figure 5.5. The number of visits that increased (black bars) or decreased (striped bars) to locations where interactions occurred between individuals in each dyad. Individuals that were categorized as territorial (individuals 1, 11, and 13) increased or decreased at the same rate. Evasive individuals (#s 2, 3, 4, 5, 6, 9, 10, 12, and 14) all decreased the number of visits to interaction locations more than they increased visits. Territorial individuals differed from evasive individuals (G-test of independence, n=14, p<0.001). Individuals #7 and 8 (dyad #4) were excluded from the analysis since they only had one interaction.

The territorial individuals were compared with the evasive ones to examine if the two groups differed in the number of visits to interaction locations. Although the evasive individuals varied in their behaviors, they were pooled since they all decreased the number of visits to areas where they encountered another individual. Territorial individuals differed significantly from the evasive ones (G-test of independence, n=14, p<0.001). Territorial individuals avoided or returned to interaction locations at the same rate while evasive individuals avoided them.

Outside interactions (when individuals encountered individuals other than their dyadic neighbor, i.e., at the fence boundaries) were not statistically tested, but 38 interactions occurred. Individual behavior coincided with inside dyad behavior; if an individual was territorial, it was territorial at its borders and vice versa. There was one case where an individual was classified as evasive, but displayed territorial behavior in three outside interactions and was evasive once. This was one of the individuals that displayed territorial behavior in half of its encounters, but still decreased visits to encounter locations.

Discussion

Rank within dominance hierarchies has been hypothesized to be established based on either physical attributes or prior experience (Whiteman & Cote 2004). I paired individuals with similar-sized (<2mm shell length difference) conspecifics to limit the physical effect. Dominance is defined as repeated agonistic encounters within a dyad where there is a consistent winner and loser (Drews 1993, De Vries 1998). In three of the seven dyads, there was a clear winner and a clear loser when one of the individuals was territorial. In dyads with two evasive individuals, an individual's overall behavior was independent of its counterpart's behavior. There was no consistent winner or loser in dyads with two evasive individuals. Four of the seven dyads contained two evasive individuals. Evasive individuals did not alter their behaviors and both remained evasive when paired with another evasive individual. Individual variation occurs in other organisms, Downes and Bauwens (2004) found that dyads with evenly-sized lizards varied in their dominance status, ranging from both individuals being tolerant to a clear dominance hierarchy.

The predetermined evasive behavior suggests that prior experience may play a role in the behavior of *L. gigantea*. Wright and Shanks (1993) were able to train *L. gigantea* to be either territorial or evasive by mimicking territorial wins or losses. After two weeks of training, they switched trainings, individuals that were trained to be territorial were subjected to losses while evasive individuals received territorial wins. Both sets of limpets switched their behaviors (territorial individuals became evasive and vice versa) but it took more time for evasive individuals to display territorial behavior. The current experiment ran for six weeks, so it is possible that one of the evasive individuals within dyads containing two evasive individuals would, over a longer time frame, switch its behavior to territorial.

Lottia gigantea has been shown to reach a certain size threshold and switch from male to female (Wright 1989, Fenberg 2008). This sequential hermaphroditism is typically accompanied by a change in behavior; evasive males become territorial females. What is not know is how closely coupled the two events are. Wright (1989) found that when the intraspecific density decreased, the likelihood of sex change increased, but there was a 1-2 year lag between territory acquisition and sex change. The sex of each *L. gigantea* was not determined prior to the beginning of this experiment. *Lottia gigantea* can be non-fatally sexed (Wright & Lindberg 1979), but I was concerned about potential stress factors associated with extracting gonadal tissue from individuals. While females tend to be territorial, Wright (1989) examined *L. gigantea* behavior in the field and found territorial males and evasive females in addition to evasive males and territorial females. There is a possibility that some individuals in this experiment were male and evasive, but all but two individuals displayed at least some territorial behavior. Sex may have influenced the amount of territorial behavior an individual displayed.

An individual's dominance status was independent of its dyadic neighbor's behavior if the individual was evasive. This is similar to the Game Theory model where an individual is considered a Hawk or a Dove (Smith 1974, Maynard Smith 1976, 1979, Maynard Smith 1982). A Hawk will fight until injured or its opponent retreats while a Dove will display, but retreat when its opponent fights. Individuals were overwhelmingly dove-like and were evasive in the majority of their interactions. If an individual was a 'dove,' it remained a 'dove' throughout the experiment and if the individual was a 'hawk,' it was territorial in the majority of its interactions. Despite the majority of the individuals being classified as evasive, all evasive individuals displayed territorial behavior at least twice, with the exception of the dyad where the individuals interacted once and the overall behavior of each individual thus could not be determined.

The location of the interaction was examined to determine whether encounters occurred at specific locations. Interactions between individuals were haphazardly distributed throughout the shared home ranges. Stamps and Krishnan (1999) suggest that individuals will avoid areas where they experience agonistic encounters, but only evasive *L. gigantea* had a tendency to decrease visits to areas where they had agonistic interactions. Territorial individuals avoided or returned to locations where they encountered another individual at the same rate.

Another prediction by Stamps and Krishnan (2001) is that the amount of home range overlap is dependent on the duration and intensity of agonistic interactions. While the duration of the interactions was usually less than one minute, the type of interaction was often a fight, where one individual would shove while the other individual would quickly retreat. Despite this, six of the seven dyads had considerable home range overlap, even in the three dyads where one individual was territorial. It appeared that individuals were not defending a fixed boundary, but defending the current space where they were located. If individuals were present in the same space at the same time, an agonistic interaction occurred. This behavior is a combination of scramble and contest competition (Parker 2000, Pellegrini 2008, Lomnicki 2009). Scramble and contest competition can be considered opposite of sides of the continuum and *Lottia* behavior falls somewhere in the middle. There was equal resource allocation in that both individuals in a dyad were free to roam wherever they decided (scramble), but if they encountered one another there was a contest with clear winners and losers.

Bridge IV

In Chapter V, I examined how *Lottia gigantea* establish territories and examined social dominance within dyads. In Chapter VI, I look further into territorial behavior by determining if *L. gigantea* returned to areas where it experienced agonistic losses.

CHAPTER VI

LOTTIA GIGANTEA RATE OF RETURN BASED ON AGONISTIC ENCOUNTERS

Introduction

Will an organism return to an area that is part of its territory if it repeatedly experiences territorial losses at that location? Stamps and Krishnan (1999) suggest that organisms should not. The model proposed by Stamps and Krishnan (1999) integrates spatial learning and behavioral ecology to examine territory formation. By suggesting that prior experience can influence where an individual establishes a territory, this model emphasizes that experience prior to territory establishment is critical. There may be a lag between the time an individual arrives at a new site and when it demonstrates territorial behavior. The individual may be collecting information about its surroundings and assessing habitat quality. Whether or not the individual experiences agonistic encounters at the site may also influence if the individual establishes a territory. All of these factors that occur prior to territory formation are based on the individual's learning ability.

One assumption (Stamps and Krishnan 1999) is that affiliative experiences increase the likelihood that an animal will return to an area while agonistic experiences will decrease the possibility that the area will be revisited. Over time, an organism will learn to avoid areas where it experiences costly encounters. The attractiveness of an area may depend on an individual's familiarity with it; the more familiar it is, the more appealing it may be. If the individual begins to experience agonistic encounters at this location, the individual may avoid or abandon the area, especially if there is adjacent available space in which to expand its territory. This avoidance may occur even if the individual is the territory owner, since the costs of defending an area may outweigh the risks of exploring new novel habitat.

An organism can learn to avoid an area where it has agonistic encounters, as long as the encounter is not fatal (Ferrari et al. 2008, Paulissen 2008, Agterberg et al. 2010). This learned behavior can aid in survival, allowing an organism to minimize the risks of predation, costly fights or detrimental abiotic factors such as unsafe terrain (Cain et al. 2008, Masuda & Aou 2009, Agterberg et al. 2010, Hertel & Eikelboom 2010). For example, rainbow trout respond either proactively (leaving the area) or reactively (engaging in submissive behavior) when exposed to a predator (Carpenter & Summers 2009). When rainbow trout were repeatedly exposed to a predator and a small escape hole was available, the individuals that learned to escape showed a dramatic improvement in escape time over the course of a week. Improvement in escape time demonstrates an ability to learn, which enhances survival rate. Through a series of agonistic encounters, crayfish established a dominance hierarchy; they were able to learn their status in the dominance order when given visual and olfactory cues (Delgado-Morales et al. 2004). More subordinate crayfish could avoid escalated and costly encounters when interacting with dominant crayfish. The freshwater snail *Physa acuta* has demonstrated an ability to avoid specific predators based on prior experience, seeking cover when exposed to fish and moving to the surface when crayfish were present (Turner et al. 2006). Wild snails, i.e., those exposed to predators in a pond, had a stronger response than captive-reared snails when exposed to crayfish, one of their predators.

Lottia gigantea, the owl limpet, can only avoid or defend itself against its predators (oystercatchers and humans) by clamping down onto the substrate, but may have learned behavior to avoid costly encounters with territorial neighbors (Lindberg et al. 1998, Kido & Murray 2003). *Lottia gigantea* is a protandrous limpet, switching from male to female when it reaches a certain size threshold (Wright & Lindberg 1982, Fenberg 2008). Small males are typically non-territorial, while larger females will defend a territories against intruders to protect algal resources (Stimson 1970, 1973, Wright 1982). When a territorial *L. gigantea* encounters an intruder, it will either push and pursue the trespasser to the edge of its territory or attempt to knock it off the substrate, resulting in probable death for the intruder as it gets washed away. *Lottia gigantea* has demonstrated behavioral plasticity when subjected to agonistic victories or losses, suggesting that previous encounters play a role in subsequent behavior (Wright & Shanks 1993). Wright and Shanks mimicked territorial wins and losses and found that when an individual was subjected to territorial losses for two weeks, its subsequent behavior was evasive, but if it experienced territorial wins for two weeks, it exhibited territorial behavior in subsequent agonistic encounters. After the two weeks the encounters were reversed; individuals who initially experienced losses then experienced wins and vice versa. Wright and Shanks noted that the individuals switched their behaviors, but individuals that were subjected first to losses and then wins changed their behaviors from evasive to territorial much slower than the individuals that first experienced territorial wins and then losses.

In this study, I hypothesized that *L. gigantea* would avoid areas where they experienced agonistic encounters. *Lottia gigantea* established home ranges over 3 weeks;

it takes 2 weeks for *L. gigantea* to establish a territory (Stimson 1970, pers. obs.). After these 3 weeks, every time they moved onto one of two random locations at their home range periphery, they experienced a territorial loss. The questions asked in this study I asked were whether or not *L. gigantea* exhibits learned behavior by avoiding areas where it experienced an agonistic loss and whether it expands its territory when subjected to agonistic encounters on the periphery of its defended home range.

Materials and Methods

Collection and Acclimation

Lottia gigantea were collected in Orange, California in April 2009 and shipped overnight to Charleston, Oregon. Limpets were allowed to acclimate for a week in the laboratory. After one week, the limpets displayed the same behaviors in the lab as in the field, ensuring that transportation did not affect their behavior. These behaviors include foraging while splashed by sea water and remaining stationary when not splashed. Limpets were kept in sea tables on unglazed terra cotta tiles covered in a biofilm. Limpets are macrophaguous grazers and will graze on cyanobacteria, diatoms and macroalgal propagules that grow on tiles (Underwood 1979, Hawkins & Hartnoll 1983). The terra cotta tiles were placed in the experimental setup one month prior to the start of the experiments to ensure there was a biofilm on them. The individuals were splashed with water for 4 hours twice a day (8 hours total) using a dump tank that mimicked high tide. Four hours of wave exposure is approximately what *L. gigantea* experiences in the field. The tank would fill with water, tip over, splash the limpets and then right itself due to a counterweight system. High intensity fluorescent lights were hung parallel to the setup and the light cycle was similar to spring conditions in the field (12:12 h light:dark). A complete description of *L. gigantea* aquaculture can be found in Chapter Two.

Time-lapse Photography and Video Analysis

Individuals were photographed for 11 hours total every day (5.5 hours for each high tide) for fifty days. Although the high tide lasted four hours, the extra 1.5 hours of footage after the high tide ended was to ensure that all movement was captured. *Lottia gigantea* does not move when it is not splashed by waves, but it will continue to move after the tiles stop being splashed but they are still wet (Stimson 1970, Wright & Shanks 1993, pers. obs.). Photos were taken every 15 seconds using a Nikon camera connected to a Digisnap time-lapse controller (Harbortronics, Inc. Model 2100). The pictures were then converted to video using MakeAVI software (http://sourceforge.net/projects/makeavi/) and then converted to Quicktime videos using AVS Video Converter (version 6.2) and analyzed with NIH ImageJ software. Data were compiled to determine where individuals spent the most time during their active periods. A grid was placed over the computer screen and the position of each individual was scored every 10 frames, for 1320 frames, for 101 videos (~ seven weeks). Every ten frames was equal to 2.5 minutes and was the minimum amount of time it took for an individual to move from one grid to another. The grid divided each tile into quarters. An individual was considered in a square of the grid if greater than 50% of its body was in the grid. Each time an individual was in a grid it was scored with a ‘1.’ If an individual was on a line between two grids, the grid value was 0.5 for each grid it was in.

Home Range Establishment

Twelve *Lottia gigantea* (shell length 38-44 mm) were used in this experiment. Individuals were placed in the middle of equally sized individual arenas, larger than a typical territory prior to the start of a tidal cycle on the mock intertidal setup (Stimson 1970). Stimson (1970) measured *L. gigantea* territories in the field and there was a significant regression between shell length and area; individuals < 50 mm did not have areas larger than 900 cm^2. In this study, arenas were 1137 cm^2. For this study, a home range was defined as the total area used by an individual while a territory was the exclusive area used by an individual (Sih & Mateo 2001). Since each individual was placed in its own arena, the terms 'home range' and 'territory' are used interchangeably. The enclosure area was larger than a territory in the field to ensure that there was adequate divisible space for home range expansion.

Chlorophyll was measured to ensure that individuals had sufficient food and that the coverage was roughly the same for each arena throughout the experiment. Chlorophyll samples were taken before and after the experiment using the chlorophyll extraction technique to ensure that the visual estimation of uniform algal density was accurate. Two samples were taken from each arena (n=24). Samples were scraped from the tiles and extracted using ethanol and measured in a fluorometer (TD-700 Laboratory Fluorometer, Turner Designs) following standard techniques (Parsons et al. 1993).

To keep individuals inside their arenas, a dowel fence was constructed and placed over the tiles and 6 cm long dowels were epoxied to their shells (Figure 6.1). When an individual encountered the fence, the dowel prevented the individual from leaving the arena. Individuals established home ranges in three weeks. Three individuals were replaced after they died one week after being placed on the setup and these new animals established home ranges in two weeks. One individual died at the start of the training period and was not replaced. Each individual's home range was determined during the first three weeks of the experiment. The time spent on each tile was summed to determine where the individual spent the most time and this tile was considered the home scar. An organism is considered to be homing if it returns to the same location after each foraging event (Wells 1917, Galbraith 1965). In this study, individuals were considered homing if they spent at least 33% of their active time in the same spot. Typically, *L. gigantea* only move when being splashed by water and don't begin moving until twenty minutes after they are wetted by the incoming tide (Stimson 1970). The limpets were filmed for 11 hours each day and were splashed with water for 8 hours. Homing individuals were typically on their home scars for the first twenty minutes and last 1.5 hours of each filming session which accounted for 33% of the footage.

Agonistic Encounters

In the field, *Lottia gigantea* territorial behavior is distinct. The territory holder shoves its shell under the intruder and attempts to knock the intruder off the rock. Intruders range from conspecifics to other limpets. The territory holder then pursues the intruder to the periphery of its defended home range (Stimson 1970, 1973, Wright 1982). Intruder behavior is evasive. The intruder will quickly turn > 90º away from the other limpet and retreat. To mimic a territorial loss, I used a stimulus limpet was used to stage an encounter, similar to Wright & Shanks (1993).

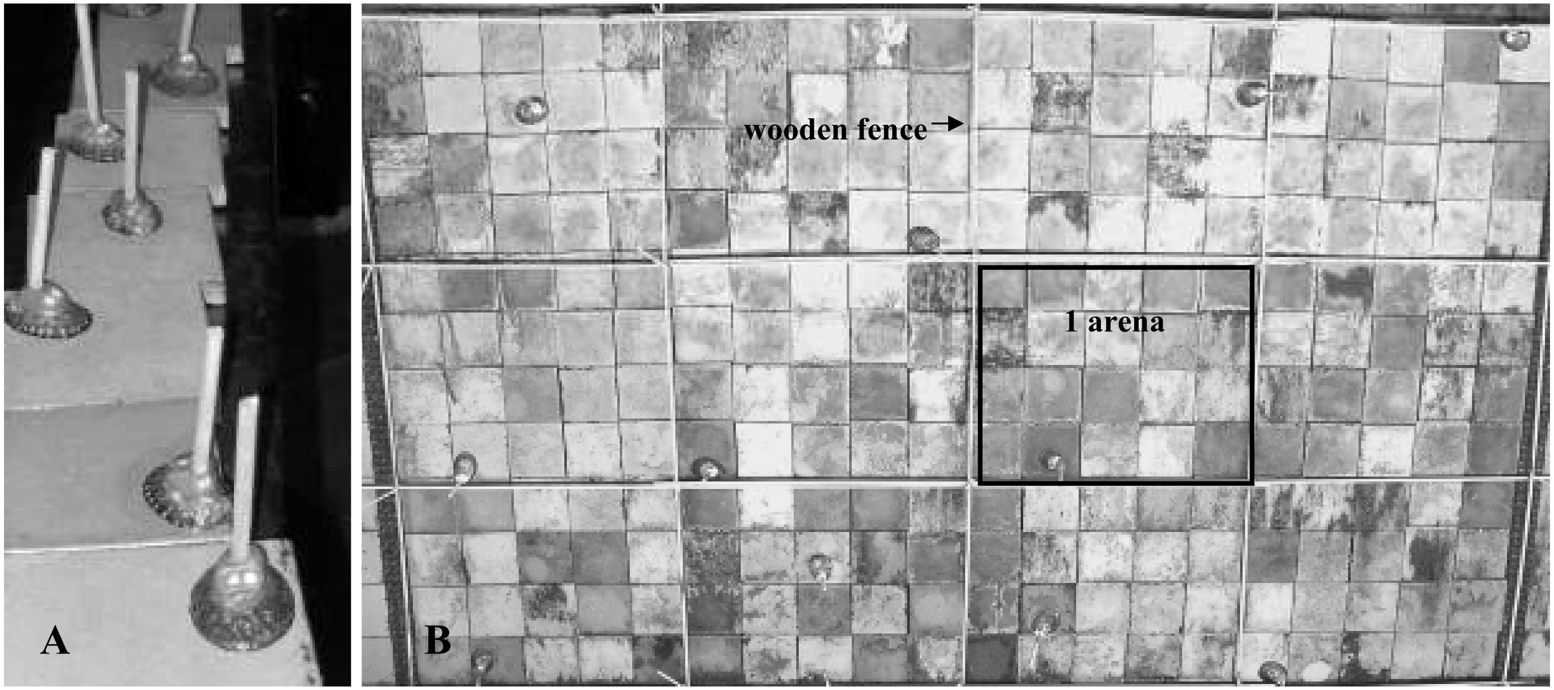


Figure 6.1. A. individuals with 6 cm dowels and ID tags epoxied to their shells. B. Experimental setup. Twelve arenas with one individual per arena. Each arena contained 20 tiles with an algal biofilm. One tile side = 7.5 cm

Stimulus limpets ranged in size from 39 - 49 cm and each individual was used no more than twice during the training period and never on consecutive days. The cephalic tentacles of the stimulus limpet were held in contact with the cephalic tentacles of the moving subject limpet for 30 seconds. When the subject limpet began to display a response, usually territorial, the stimulus limpet was used to push the subject limpet at a consistent and forceful rate. A loss was mimicked by pushing the subject limpet at a rate of 1 - 5 mm/s to the periphery of its home range for 90 seconds. The subject limpet was pushed until it retreated or clamped down and did not move. Initial behavior of the subject limpet was recorded either as evasive or territorial. An evasive response was considered a > 90º turn of the subject limpet away from the point of contact with the stimulus limpet while territorial behavior was defined as a forward movement of half the shell length of the subject limpet. After three weeks of initial home range establishment, individuals experienced an agonistic loss every time they moved onto randomly selected tiles located at the home range periphery during the night high tides. Individuals were subjected to agonistic losses for two weeks. This two week period was considered the training period. The training occurred only during the night high tide (4 hours every day). Most individuals moved during the night high tide (96%), while less moved during the day high tide (69.5%). The limpets were photographed for an additional two weeks to determine their final home ranges.

The number of visits to the agonistic tiles before training was compared to that during and after training. To compare visits among the stages (before, during and after training), the number of visits to the agonistic tiles was divided by the total number of visits per stage. The amount of time prior to the training varied for all individuals, so the ‘before’ data were set to one for each individual and the data were ranked. The amount of time for the ‘during’ and ‘after’ training was a percent of the ranked data and the amount of time among the ‘before,’ ‘during’ and ‘after’ training was compared in a nonparametric two-way ANOVA without replication (SAS version 9.2). The amount of area each individual used throughout the experiment was compared using the same method. Two individuals died during the experiment and were excluded from the analysis. Data from the individual who died at the end of the experiment were used in totaling the number of agonistic encounters.

Results

The experiment ran for seven weeks and was divided into three stages: before, during and after training. The ‘before’ stage lasted three weeks while the ‘during’ and ‘after’ training were each two weeks long. One individual died prior to the start of the training and another individual died during the ‘after’ training period in the second week. The chlorophyll concentrations were 0.37 $\mu g/cm^2 \pm 0.08$ and 0.60 $\mu g/cm^2 \pm 0.12$ (mean ± SE) before and after the experiment, respectively. Concentration did not change over time when the chlorophyll concentrations were compared prior to start of the experiment and after (Unpaired t test, df=46, t=1.5, p=0.13). It was assumed that the food supply was constant since the chlorophyll concentrations did not change significantly over time.

Limpet movement was analyzed to determine if individuals established home ranges prior to training. Individuals were considered to have home ranges if they formed home scars, demonstrating a preference for a certain locations. A home scar was an area where an individual spent > 33% of the time captured on video. All individuals formed a home scar prior to the training, returning to the exact location after each foraging bout. Individual arena usage ranged from 22% to 76% of the total area available. This was determined by calculating the total home range area for each individual and dividing by the total available area (1137 cm^2).

After three weeks, individuals were subjected to agonistic losses each time they crossed onto two randomly selected tiles at the periphery of their home range. There were 60 staged interactions total, with all eleven individuals crossing onto the agonistic loss tiles at least twice on separate occasions, with an average of 5.5 encounters per individual during the two weeks of training. Only one individual showed evasive behavior when presented with an intruding limpet, while one other individual was evasive during its first two agonistic encounters but demonstrated territorial behavior when it crossed the agonistic tiles three more times. The nine remaining limpets displayed territorial behavior every time they were confronted with the stimulus limpet on the agonistic loss tiles.

To ensure that that size of the stimulus limpet did not affect the behavior of the subject limpet, stimulus limpets were divided into two categories: small and large. The shell length of small stimulus limpets was less than the average size of the subject limpets and large stimulus limpets shell length was greater than the subject limpet average shell size. The initial reaction (territorial or evasive) of the subject limpet was compared to the size of the stimulus limpet (small or big). There was no difference between the two sizes of stimulus limpet (G test for independence, $x^2=0.62$, $p = 0.73$).

The number of visits to agonistic treatment tiles was compared before, during and after the training for each individual. The percent of visits to agonistic tiles compared to visits total prior to treatment varied considerably and the ‘before’ visits were standardized to 1 in order to compare the number of visits during and after the training. Prior to the training, individuals visited the agonistic tiles an average of 6.85 % ± 1.85 (mean ± standard error) of the time based on the total number of visits. The number of visits was expected to decrease if *Lottia gigantea* showed learned behavior and learned to avoid tiles where they experienced agonistic losses. Based on the total number of visits, individuals visited the agonistic tiles 3.01% ± 1.29 of the time during the training period and 2.36% ± 1.02 of the time after the training period. Visits to agonistic tiles decreased both during and after the training period, but there was a trend when the number of visits was compared between the before and after the training period (Figure 6.2, 1 way ANOVA with multiple comparisons, n=10, F= 4.16, p=0.056). One individual increased its visits to the training tiles during the agonistic encounters, but then decreased visits to the agonistic tiles once the training stopped. Overall, the individuals visited the agonistic tiles with less frequency than prior to the training when the number of visits to the agonistic tiles was compared among the before, during and after training. Eight individuals decreased the amount of time spent on the agonistic tiles before and after the training. The two individuals that increased visits to the agonistic tiles during the training did not visit the treatment tiles much during the three weeks prior to encounters (0.09% and 0.04% of each individual’s total number of visits was spent on the treatment tiles prior to encounters).

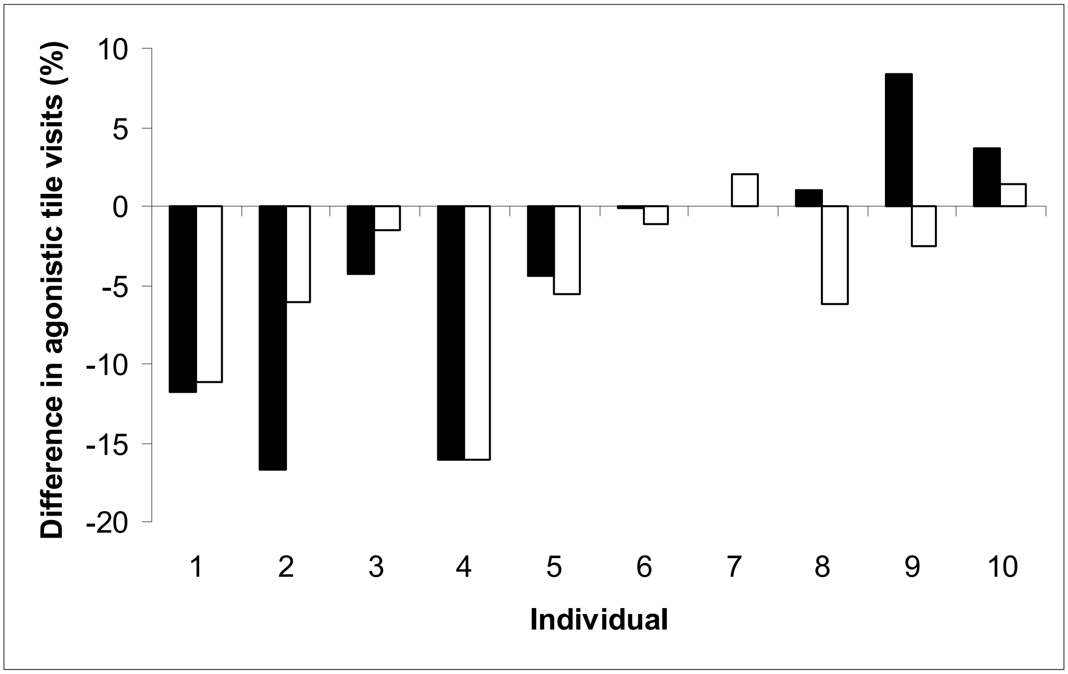


Figure 6.2. Visits to agonistic tiles based on total number of visits. The difference between agonistic tile visits was compared for before minus during training (black bars) and between the before minus after training periods (white bars). Six individuals decreased visits during the training period while eight individuals reduced visits to agonistic tiles after the training period (1-way nonparametric ANOVA, F=4.16, p=0.056, comparing before and after, n=10).

When individuals' home range areas were compared, six individuals spent more time in the same areas during the training, but increased their home range area once the training stopped (Figure 6.3, 1-way ANOVA with multiple comparisons, n=10, F=6.95, p<0.05). Most individuals compressed their home range area during the agonistic encounters period. One individual did not alter the size of its home range throughout the seven weeks and three individuals expanded their home range sizes. Eight individuals expanded their home ranges by 5% after the training period, but the proportion of tile area used was about the same when before the training period was compared to after the training. One individual reduced its home range area by half and did not expand it after the training.

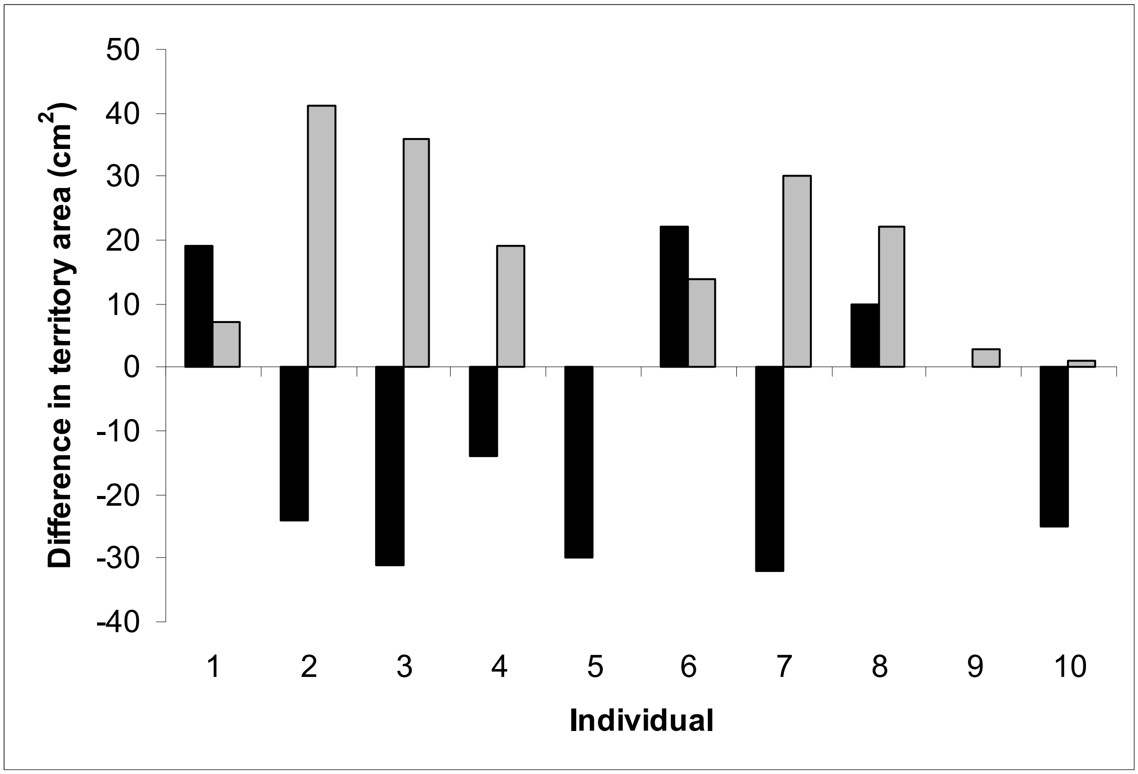


Figure 6.3. Territory size based on the size difference each individual traversed before minus during training (black bars) and during minus after the training period (gray bars). Individuals significantly reduced territory size during the training (2-way nonparametric ANOVA, F=6.95, $p<0.05$ for during, n=10). Territory size decreased for six individuals during the training and increased for nine individuals after training.

Only one individual did not form a home scar during the training period. Home scar locations were classified as staying in the same location, moving, and moving away from the agonistic tiles. If an individual moved its home scar $\geq$ 1 tile away from the agonistic tiles, it was considered moving away from the agonistic tiles. Of the nine that formed a home scar, seven moved their home scars to a new location during training. Four individuals moved their home scars away from the agonistic tiles while they were experiencing territorial losses. During the two weeks after the agonistic losses, all 10 individuals formed home scars. Seven individuals relocated their home scars and 4 limpets moved away from the agonistic tiles despite not being subjected to agonistic losses during this time frame. Whether an individual formed a new home scar or moved its home scar away from the agonistic tiles was compared, but these results were not significant (G test for independence, x^2=0.03, p=0.99).

The number of agonistic interactions was pooled to determine if individuals visited agonistic tiles less over time. The number of visits did significantly decrease (Figure 6.4, Regression, R^2=0.58, F=16.94, p=0.001)). None of the individuals moved onto the agonistic loss tiles on the last two days of the training. The number of encounters appeared to increase on days 9 and 11, but this was due to one individual that consistently returned to the agonistic loss tiles.

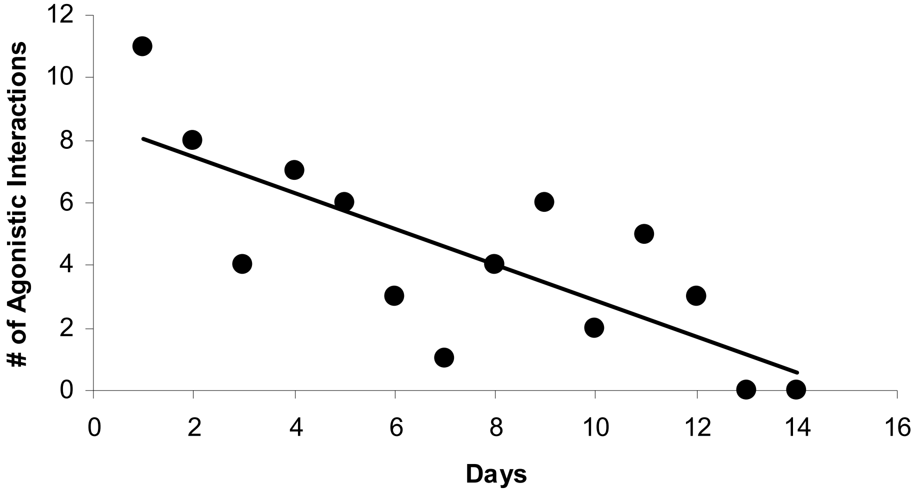


Figure 6.4. Total number of agonistic interactions over time. The total number of agonistic interactions each day was summed for all individuals (n=11). The number of interactions decreased significantly over time (Regression, R^2=0.58, F=16.94, p=0.001).

Discussion

If the limpets behaved as predicted by the Stamps and Krishnan model and showed learned behavior, individual *Lottia gigantea* would shift their home ranges away from the areas where they experienced agonistic losses. *Lottia gigantea* appears to have learned behavior, but it is more complex than model predictions. Stamps and Krishnan (1999) assume that the attractiveness of an area is dependent on the positive and negative experiences an individual has at certain locations and these experiences are independent of each other. They predict that if an individual has repeated agonistic encounters at the same place, it will abandon that area and move to an unfamiliar area, regardless of whether the individual was a resident or newcomer. Morrell and Kokko (2003) suggest that avoidance is adaptive in cases where the cost of fighting outweighs the benefits of the area. An individual should only return to an area where it has not experienced repeated agonistic interactions. I found that *L. gigantea* did avoid areas where they experienced agonistic encounters, but did not necessarily expand their territories during or after the training period.

While *L. gigantea* did avoid the agonistic tiles during the training, they did not necessarily shift their home ranges away from the agonistic tiles. Individuals compressed the size of their territories during the two weeks of agonistic encounters, despite having additional space in which to expand their territories. Individuals avoided the agonistic encounter tiles and did not traverse as much area as they did prior to the training. Once the training ended, individuals expanded their home ranges to sizes equivalent or larger than the size before training, but continued avoiding the agonistic encounter tiles.

Individuals formed home scars throughout the training process but shifted their home scars during and after the training. Although the shifting of the home scar was not significant, individuals express home scar fidelity in the field and laboratory (Stimson 1970, pers. obs), and the home scar location shifting may have been caused by being subjected to agonistic losses.

A range of behaviors was displayed by individuals, suggesting that *L. gigantea* behavior is plastic and dependent on many variables, such as food resources and tidal cycle. Variation in food resources and tidal cycles could contribute to behavioral variation, but the food supply and tides were consistent throughout this study. *Lottia gigantea* will expand its territory if the food density decreases and decrease its territory if food is abundant (Stimson 1973). Stimson removed algae from *L. gigantea* territories in the field and individuals enlarged their territories. In the case of my experiment, the algal biofilm on the tiles was uniform across the experimental setup. Tidal cycle also affects *L. gigantea* behavior. Stimson (1970) found that *L. gigantea* would only move when being splashed with water, beginning to graze 20 minutes after being wetted by the rising tide. Wright and Nybakken (2007) showed that *L. gigantea* movement was influenced by substantial wave action; *L. gigantea* decreased movement when the maximum wave height exceeded 1 m. In the experimental setup described herein, individuals consistently moved and were not affected by the wave action, as the experimental setup mimics a moderate splash zone.

The variance in *L. gigantea* behavior implies a plasticity enabling adaptation to a changing environment. When *L. gigantea* experienced agonistic encounters at the same locale, it avoided that location, suggesting that *L. gigantea* does have learned behavior.

Additionally, a majority of the individuals compressed the size of their home ranges during the training period. When the agonistic encounters stopped, *L. gigantea* continued to avoid the agonistic encounter location, but they increased the size of their home ranges. In terms of the Stamps and Krishnan model (1999), individuals learned to avoid the area where they experienced agonistic losses, but individuals did not expand their home ranges into novel area during the training period and actually reduced the size of their home ranges during that period.

In a study by Wright and Shanks (1993), *L. gigantea* was subjected to staged territorial encounters and they found that the behavior of *L. gigantea* depended on prior experience. *Lottia gigantea* was territorial if it had territorial wins, but evasive if it experienced a territorial losses. When these behaviors were switched, territorial individuals experienced a territorial loss and displayed evasive behavior, and evasive individuals became territorial when they experienced a territorial win. In this study *L. gigantea* always experienced a territorial loss. With the exception of one individual, all individuals displayed territorial behavior after two weeks of training despite receiving losses for two weeks. The number of losses per individual may have not been enough to alter their behaviors to evasive ones.

Other limpets displayed behavioral plasticity while foraging. *Patella vulgata,* a northern Atlantic limpet, varies when it forages based on tidal cycle, substrate inclination and season (Santini et al. 2004). Santini et al. (2004) suggested that these discrepancies were caused by *P. vulgata* responding to environmental cues; when individuals foraged depended on a combination of the diel and tidal cycles and rock slope. Shanks (2002) trained *L. gigantea* to be territorial or evasive and found that territorial individuals grazed more prudently than evasive individuals, territorial animals left behind 71% algal cover behind compared to 50% left behind by evasive individuals.

Learned behavior is thought to be a special form of behavioral plasticity (Stephens 1991), allowing an organism to switch its behavior quickly, depending on its experience. Both intrinsic and extrinsic factors influence learning, as an animal must have the capability to collect and manage information while balancing the costs of not being able to assess extrinsic factors such as unnoticed predators (Komers 1997). Learned behavior has evolved in a variety of organisms, indicating that it can be an evolutionarily advantageous trait.

In the case of *L. gigantea*, learned behavior appears to have evolved as an avoidance mechanism, allowing it to avoid areas that present too many costs when visited. In the field, territorial *L. gigantea* may form contiguous territories with its territorial neighbors. If a territory holder encounters another territory holder, a fight may occur. A fight is both energetically costly and could result in death if one of the territory holders is knocked off the rock. By learning to avoid such areas, *L. gigantea* reduces its energetic costs and increases its probability of survival.

Bridge V

I examined whether or not *Lottia gigantea* has learned behavior in Chapter VI. In Chapter VII, I test if *L. gigantea* can differentiate between its own mucus and a conspecific's mucus.

CHAPTER VII

LOTTIA GIGANTEA MUCUS TRAILS AS TERRITORY MARKERS

Introduction

Many studies have examined the various roles of gastropod mucus with a focus on its ability to serve as aid in locomotion and adhesion, an environmental indicator, settlement cue, defense mechanism, prey capture, algal cultivation, and trail following device (Wells & Buckley 1972, Townsend 1974, Denny 1980b, Connor & Quinn 1984, Connor 1986, Smith 1991, Davies & Beckwith 1999, McQuaid et al. 1999, Davies et al. 2005, Ribak et al. 2005, Lairnek et al. 2008). What has not been examined is the potential role of mucus trails as territory markers. Many organisms use chemical communication to indicate a social status or a territory, such as deer, rabbits, and wolves (Miller et al. 1998, Sillero-Zubiri & Macdonald 1998, Vache et al. 2001). Chemical communication can be a stable and long-lasting signal, which is advantageous to a territory holder that cannot easily monitor its entire territory. *Lottia gigantea*, the territorial owl limpet, has been shown to chase intruders to the perimeter of its territory without crossing over into non-territory, suggesting that the territory boundary is demarked (Stimson 1970). It is not known how *L. gigantea* recognize their territory boundaries relative to those of conspecifics. Stimson (1970) observed territorial *L. gigantea* push intruders off their territories, but would never pursue the intruder for more than a few centimeters past the edge of their territory. Therefore, some mechanism should be present to indicate boundaries for *L. gigantea.*

Mucus serves an important role in the life of a gastropod, ranging from locomotion to feeding and protection. The primary function of mucus is locomotion;

gastropods must first secrete a thin layer of mucus before they can crawl forward. The energetic cost of locomotion in terms of mucus production alone is 9 – 26 % of assimilated energy (Denny 1980a), representing a major sink in gastropod energetics. This energetic cost lends itself to the examination of other potential mucus functions. The mucus trails of gastropods have been examined in terms of home site location and home scar formation, foraging routes, desiccation reduction, energetics, and predator avoidance (McFarlane 1980, Bretz & Dimock 1983, Horn 1986, Davies et al. 1992a, Davies et al. 1992b, Davies & Williams 1995, Davies & Hawkins 1998). While some gastropods can follow conspecifics' mucus trails, it is not known if *L. gigantea*, a territorial limpet, will avoid a conspecific's mucus trail.

Homing gastropods appear to follow their own or other conspecifics mucus trails (Wells & Buckley 1972, Townsend 1974, McFarlane 1980, Bretz & Dimock 1983, Davies et al. 1992b, Davies & Beckwith 1999, Hutchinson et al. 2007). Trail following behavior may serve to reuse the energy-rich mucus. Work done by Connor and Quinn (1984) and Connor (1986) suggested that the mucus by several limpets species traps microalgae and stimulates algal and bacterial growth. These studies found that the mucus of *L. gigantea*, a territorial and homing limpet, and *L. scabra*, a homing limpet, served to stimulate microalgal growth and increase adhesion of microalgae when compared to the mucus of both a non-homing limpet and a carnivorous gastropod. A comparison of lab and fieldwork confirmed that the mucus of both homing limpets was more adhesive than that of a non-homing limpet, meaning that the mucus was able to trap algae more effectively. In addition, mucus sheets laid down by homing limpets persist over longer periods. Davies et al. (1992a) demonstrated that the mucus of *Patella vulgata*, an eastern Atlantic homing limpet, had an ability to trap microalgae as well.

Gastropods vary in their ability to interpret a mucus trail and the information found in the mucus, ranging from navigation to following conspecifics' trails in order to aggregate and prevent desiccation (reviewed by Davies and Hawkins 1998). The predatory opisthobranch, *Navanax inermis*, follows the trails of its prey (as cited by Bretz & Dimock 1983), but cannot detect its direction, while the marine mud snail, *Ilyanassa obsoleta* can detect the polarity of conspecific's trails, preferring to follow the trail in the direction in which it was laid (Bretz & Dimock 1983). The marine pulmonate, *Onchidium verruculatum*, leaves its home, a hole or a crevice in the rocks, to feed at low tide and follows its own mucus trail back to its home, but does not always home with the use of the outward mucus trail (McFarlane 1980). Although there is much speculation as to whether or not a gastropod can detect both the presence and polarity of a trail, the actual mechanisms mediating recognition of mucus trails are still largely unknown. Speculation includes a response to the chemical cues found in the mucus via contact chemoreception.

My goal was to determine whether *L. gigantea* behavior changes when it encounters mucus from a non-neighboring conspecific. After individuals established territories on tiles in the laboratory, four tiles were switched in each arena, two tiles from a non-neighboring conspecific and two tiles with no mucus on them. Tiles were selected from non-neighboring conspecifics as a 'dear enemy' effect has been noticed among neighboring *L. gigantea* (pers. obs.). The 'dear enemy' effect arises when neighboring territory holders are less aggressive towards one another (Getty 1987, Temeles 1994).

Lottia gigantea behavior was examined to see if individuals spent less time on tiles with either no mucus or conspecific's mucus compared to tiles with self mucus. The role of an algal film was investigated by determining if *L. gigantea* had a behavioral change in response to just mucus, no algal film on the tiles, either from itself or a conspecific.

Materials and Methods

Husbandry

Lottia gigantea were collected from Orange, California in February, 2010 and shipped to Charleston, Oregon. Individuals were placed on the experimental setup and allowed to acclimate for one month. This was to ensure that the limpets' behaviors were similar to those in the field and individuals were healthy. Natural behavior of *L. gigantea* is that individuals will forage when being splashed with water. If an individual is not healthy, it will move little and dies within a few days of stopping movement (pers. obs.). Individuals were placed on unglazed terra cotta tiles on a sloped sheet of plywood in sea tables. To mimic the tidal cycle, a water timer was hooked up to a flow-through seawater system which ran for four hours, twice a day, simulating a semidiurnal tide. The waves were generated by a dump tank located above the plywood frame. The dump tank was connected to the sea water system; the dump tank would fill with water, tip over splashing the individuals with water and then right itself via a counterweight. *Lottia gigantea* live in the splash zone of the rocky intertidal and four hours is typically the amount of time organisms in this zone are exposed to water. Algal growth on the tiles was promoted by a high output fluorescent system. Limpets are macrophagous generalist grazers and will scrape the biofilm found on rocks ((Underwood 1979, Hawkins &

Hartnoll 1983). The lights were on a 12:12 light:dark cycle to mimic natural seasonal conditions. For complete details of *L. gigantea* husbandry, see Schroeder (Chapter 2).

Territories with Algae Experiment

Twenty-four individuals were used and two equal-sized individuals were placed in an arena, with a total of 12 arenas and 24 individuals on March 14, 2010 (Figure 7.1). Two individuals were placed in each arena to ensure that individuals established territories. The experiment ran until April 12, 2010. Individuals were between 3.4 and 4.1 cm in length. The arenas were equal in size and slightly smaller than twice the average territory (territory size is correlated to limpet length in the field (Stimson 1970)). The arenas were constructed by making a frame from wooden dowels. Individuals were restricted to their arenas by 6 cm long dowels vertically epoxied to their shells. When an individual encountered the edge of the arena, the epoxied dowel prevented it from moving into another arena.

Chlorophyll samples were taken to ensure that the food source was evenly distributed on the experimental setup. Algal density was estimated by visual approximation, i.e., did the tiles appear to have an even coating of algae on them and confirmed by taking two random chlorophyll samples from each arena (n=24), scraping a corner (~3.9 cm^2) of a randomly selected tile and using standard chlorophyll extraction techniques (Parsons et al. 1993). Samples were taken before the experiment and after the experiment and measured in a fluorometer (TD-700 Laboratory Fluorometer, Turner Designs).

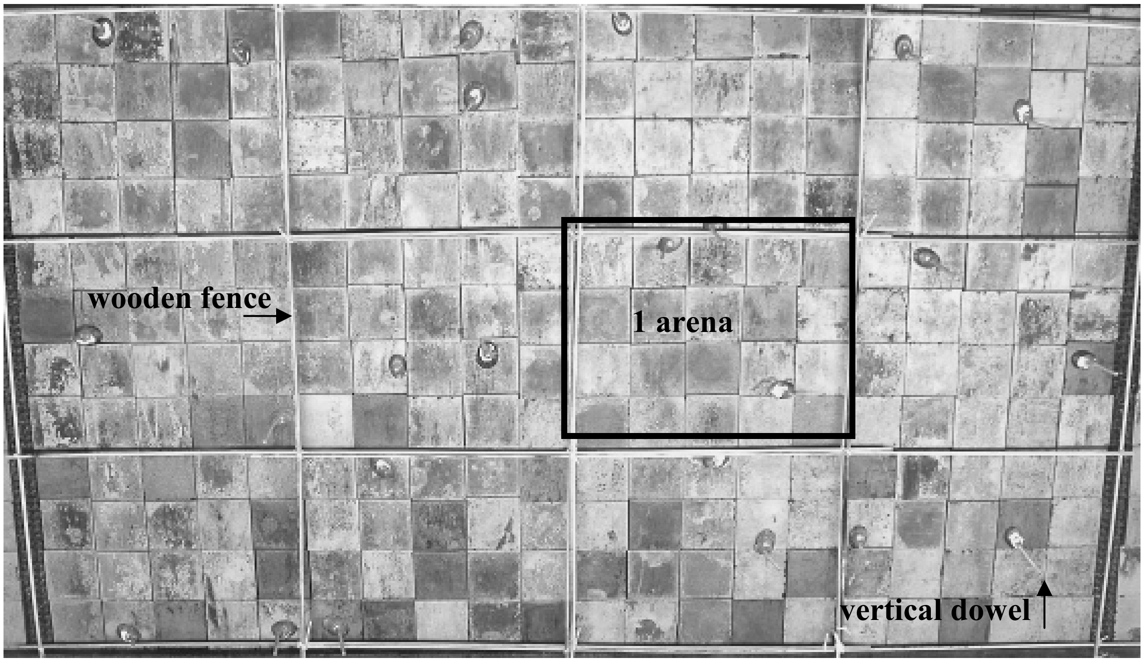


Figure 7.1. Territories with algae experiment. 12 arenas defined by wooden dowel rods and containing 20 uncoated terra cotta tiles were exposed to intermittent splashing and light for four weeks. Each arena contained two similar-sized *Lottia gigantea* (<2 mm difference). Each individual had a 6 cm dowel vertically glued to its shell. When the individual encountered the fence, the dowel prevented it from escaping.
One tile side = 7.6 cm

In the first two weeks individuals established home ranges. After one week, individuals were monitored to determine the location of their home scars and the next most visited tile. Home scars are locations limpets return to after each foraging event (Wells 1917, Galbraith 1965) and were not moved during the experiment (home scar tile). After two weeks, four tiles were switched in each corral, two treatment tiles and two control tiles (Figure 7.2). The second most visited tile was replaced with a tile that was free of mucus (= no mucus tile). The mucus-free tile was a tile placed on the experimental setup at the same time as the other tiles, i.e., had the same amount of time for algal growth as the other tiles, but no limpets had moved over them. The second most-visited tile of an individual was randomly placed in a non-contiguous arena next to another individual's home scar tile. The second most-visited tile was used as the treatment tile for another individual (= other mucus tile). It was assumed that the 'other mucus' treatment tiles were covered in mucus because they were the most frequented tiles besides the home scar tile of each individual. The switched tiles were from non-contiguous arenas because *L. gigantea* has demonstrated a 'dear enemy' effect when it encounters a neighbor (Temeles 1994). A third tile served as the self-mucus treatment tile for each individual which were the rest of the tiles that were not switched (= self-mucus tile). These tiles were adjacent to the individual's home scar, but not moved or adjusted in any way. Individuals were filmed for two more weeks to determine if they preferred a type of tile-no mucus, other mucus, self-mucus or home scar tile.

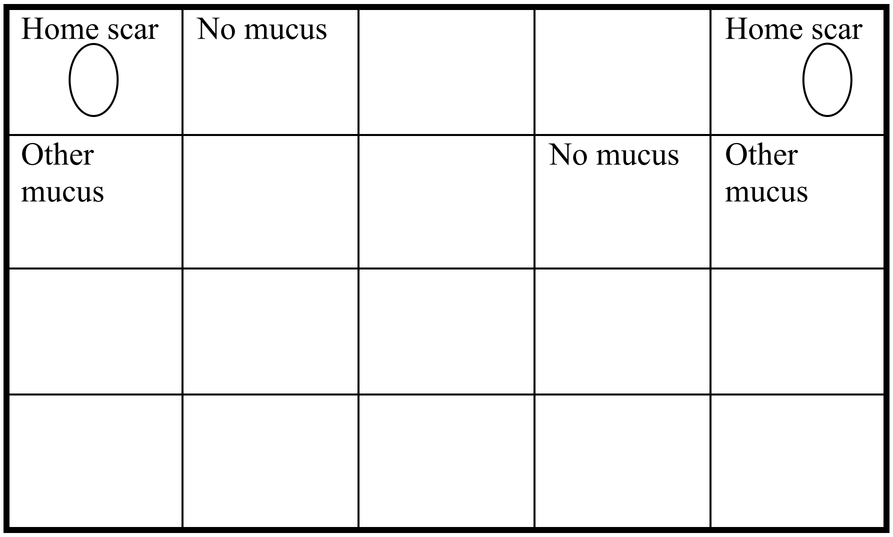


Figure 7.2. Schematic drawing of the tile switch for 'territories with algae' experiment in one arena. Four tiles were switched in each arena; two tiles without mucus (no mucus tiles) and two tiles with mucus from a conspecific (other mucus tiles). Individual home scar tiles were not moved. The remaining tiles were not altered (self-mucus tiles). The other mucus tiles were switched with the second most visited tile for each individual. The 'no mucus' tiles were randomly switched with self-mucus tiles, but placed adjacent to the home scar tile.

Two Tile Test without Algae Experiment

Twenty-one individuals were placed in arenas consisting of two tiles on August 18, 2010 (Figure 7.3). The arenas were surrounded by Astroturf to prevent them from leaving the arena. *Lottia gigantea* will not cross Astroturf (Wright & Shanks 1993, Shanks 2002). The tiles were pressure washed and scrubbed to ensure that no algae were on them. The individuals were monitored for two days (four foraging cycles) to determine whether they crossed over to the other tile. On the third day, the tile less favored by each individual was switched, i.e., the tile the individual was not on. The switched tile was replaced with one of three treatment tiles-tiles with no mucus (held without limpets), tiles with mucus from a conspecific (a tile another limpet had visited), and tiles with the individual's mucus (a tile the individual had visited). Each individual received one of three different tiles treatments. If the individual received its own tile, the individual and its tile were picked up and replaced in the same spot to mimic the procedure of tile switching for the other treatment tiles and to ensure that the physical act of moving the limpet did not affect their behaviors.

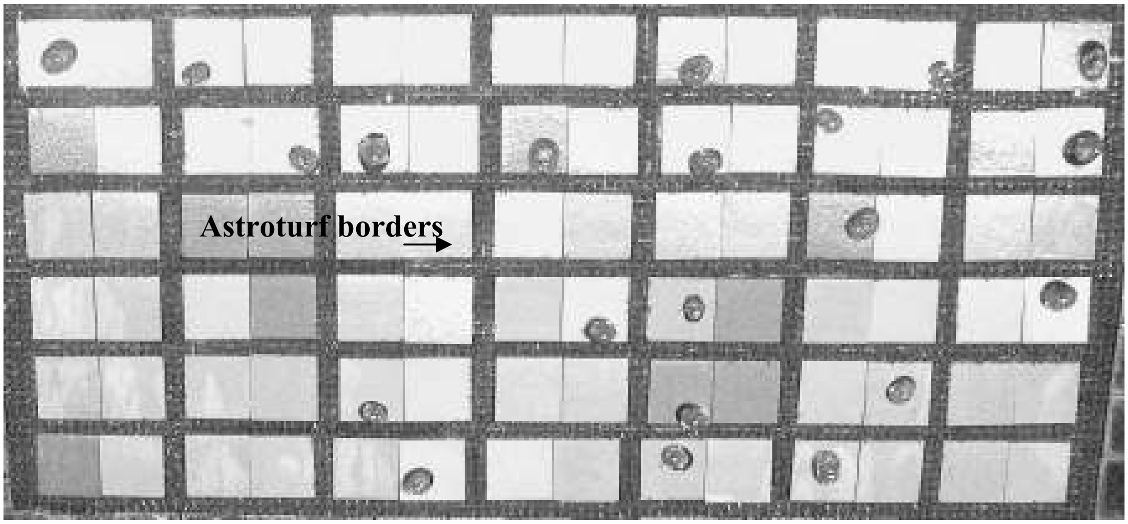


Figure 7.3. Two tile test without algae experiment. Individuals were randomly placed in arenas defined by Astroturf borders (n=21). Individuals were placed on the setup and allowed to acclimate for two days. On the third day the less frequented tile was randomly switched with one of three treatments-no mucus tiles, tiles with mucus from a conspecific (other mucus tiles) and self-mucus tiles. Individuals were monitored for behavioral changes after the tile switch.

Time-lapse Photography

During the mock high tide, limpets were photographed for four weeks using a Digisnap time-lapse controller (Harbortronics, inc., model 2100) attached to a Nikon Coolpix 5700 digital camera mounted above the experimental setup. Typically, *L. gigantea* only moves when being splashed by water and do not begin moving until twenty minutes after first being splashed (Stimson 1970). A picture was taken every 15 seconds, for 5.5 hours, twice a day. Although the high tide lasted four hours, the extra 1.5 hours of footage at the end of the high tide was to ensure that all movement was captured. *Lottia gigantea* does not move when it is not splashed by waves, but it will continue to move when the substrate is wet (Stimson 1970, Wright & Shanks 1993, pers. obs.). The pictures were converted to .avi movies using MakeAVI software (http://sourceforge.net/projects/makeavi/). AVI files were converted into Quicktime videos (AVS Video Converter 6.2) and analyzed using Image J software (http://rsbweb.nih.gov/ij/).

Data Analysis

Territories with algae experiment

During the first two weeks of territory establishment, individual locations were scored to determine which tiles were most visited. After the tile switch, the number of visits to each type of tile was scored every 10 frames, which was every 2.5 minutes, using ImageJ. To track limpet movement, a grid was constructed and placed over a computer screen that divided the tiles into quarters. An individual was considered in a square if greater than 50% of its body was in the grid. Movement data were compiled to determine where individuals spent the greatest amount of time. Visits to each tile type were scaled to the number of treatment tiles visited, i.e., the number of visits total was divided by the total number of each tile type visited. Since the tiles were divided into quadrants for the image analysis, numbers reflect the quadrants, rather than one tile. For example, if an individual visited 'no mucus' tiles 16 times and it visited 4 'no mucus' tiles total, the individual had four 'no mucus' tile visits. This was done to standardize the number of visits to each tile type since there were more self mucus tiles. The four tile types were the home scar tile, self-mucus tiles excluding the home scar, non-self mucus tiles and no mucus tiles. Each tile type was then ranked from 1-4, with the most frequented type being one and the least visited being four. One individual was eliminated from analysis because it re-established a home scar on a treatment tile and another individual died prior to the tile switch. The ranked data were analyzed using a non-parametric one-way

ANOVA with tile type as the fixed treatment and the visit ranks as the dependent variable (SAS version 9.2).

Two tile test without algae experiment

Limpets were scored as either movers or non-movers based on observations from time-lapse images. Limpets were considered movers if they crossed over to the experimental treatment tile at any time in either the one day before tiles were switched, the day the tiles were switched, or the day after the tiles were switched. I therefore compared a binomial response variable (mover versus non-mover) among tile treatments and our three time periods. The ratio of movers to non-movers was ranked based on the time and tile treatment and analyzed using a non-parametric 2-way ANOVA. The individuals were monitored to determine if they crossed over to the other tile and exhibited any noticeable behavioral changes such as tile avoidance or an increase in speed as the tile was crossed (SAS version 9.2).

Results

Territories with Algae Experiment

Prior to the tile switch in the 'territories with algae' experiment, individuals behaved normally. They established home ranges and home scars, a specific location an individual returned to after each foraging event. Individuals only foraged when the dump tank was running and they were being splashed with waves. One individual died during the first two weeks of territory establishment. Chlorophyll samples were taken at the beginning and end of the experiment (beginning measurement-0.152 $\mu g/cm^2 \pm 0.02$

(mean ± standard error) and end 0.209 μg/cm^2 ± 0.05). The amount of algae increased slightly at the end of the experiment, but the results demonstrate that the food source was consistent and the tiles were evenly covered in biofilm.

There was no noticeable change in foraging behavior after the tile switch. Individuals continued to forage in their territories and return to their home scars prior to the administration of experimental treatments. The home-scar tile was the most frequented tile for all individuals, followed by no mucus tiles, self-mucus tiles, and other mucus tiles (Figure 7.4). Pair-wise orthogonal contrasts were employed to test for specific differences among treatments. Visits to the home-scar tile were significantly higher than to any other tile type (non-parametric ANOVA, F=8.72, n=22, p=0.004). Although I expected that individuals would spend the most time on the home scar tile, the data were used to ensure that individuals continued to behave normally after the tile switch. Individuals returned to the exact location after each foraging cycle. Visits to no mucus tiles were significantly more frequent than visits to both of the mucus treatments (non-parametric ANOVA, F=127.69, n=22, $p < 0.001$). This can be accounted for since individuals spent the least amount of time on other mucus tiles. Visits to self-mucus tiles were significantly more frequent than to other mucus tiles (Figure 7.5, non-parametric ANOVA, F=6.52, n=22, p = 0.013).

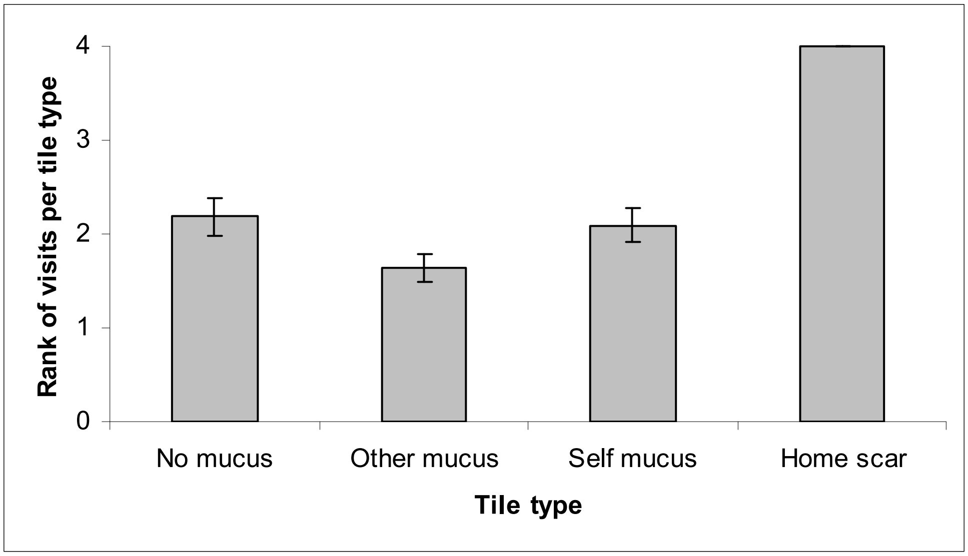


Figure 7.4. Territories with algae experiment. Four different tile types were ranked based on the number of visits to each tile type. The four tile types were tiles with no mucus, mucus from a conspecific, self-mucus and a home scar tile. Visits to each tile type were standardized based on the total number of visits to each tile type. Individuals' visits (n=22) were ranked 1 to 4 (least to most) and ranks were averaged (average ± SE).

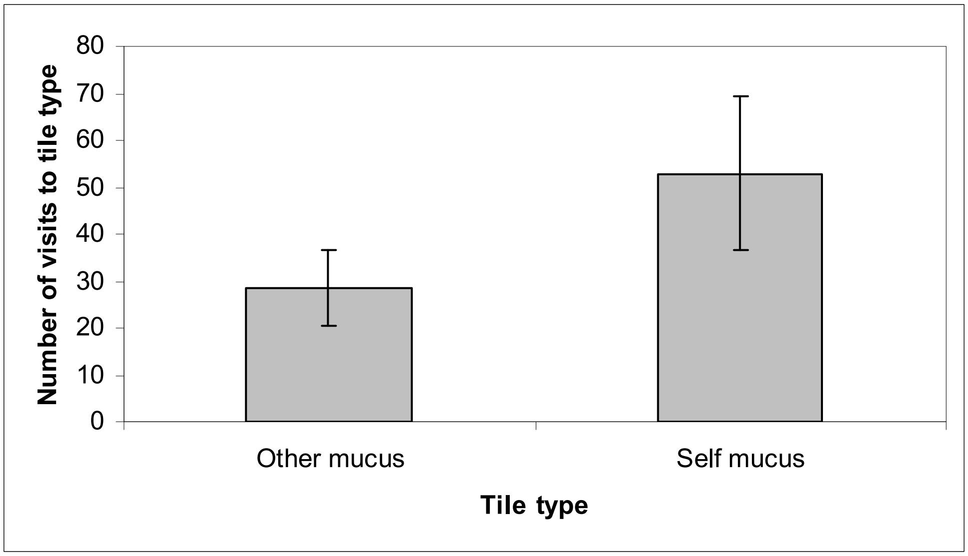


Figure 7.5. Territories with algae experiment. The number of visits to other mucus tiles compared with self-mucus tiles. Numbers were averaged for all individuals (average ± SE). Individuals significantly visited tiles with their own mucus more frequently than tiles with a conspecific's mucus (non-parametric ANOVA, F=6.52, n=22, p = 0.013).

Two Tile Test without Algae Experiment

All individuals moved during the foraging cycles prior to the tile switch on day five. Individuals were monitored to see whether they crossed over to the other tile during the first two days, which was equal to four foraging cycles. Individuals were divided into groups based on treatment-no mucus, self-mucus and other mucus. Roughly half crossed over each cycle (4 out of 7 individuals) prior to the tile switch for the no mucus and self-mucus treatments. The other mucus group crossed over at a higher rate during the first three foraging cycles (Table 7.1). Since the other mucus group crossed over the other tile at a greater rate than the other two groups, the crossing over data were ranked to standardize the baseline. The treatment type (no mucus, self-mucus, other mucus) had no effect on an individual's movement (2 way non-parametric ANOVA, F=0.10, n=21, p=0.9). Time was significant and all individuals reacted the same way, moving to the other tile with a greater frequency when tiles were switched (2 way, non-parametric ANOVA, F=4.57, n=21, p=0.03). The results suggest that the treatment didn't matter, but time did (Figure 7.6). There was no treatment*time interaction (2 way, non-parametric ANOVA, F=1.59, n=21, p=0.24).

Table 7.1. Two tile test without algae experiment. Individuals were placed on a tile in individual arenas with two tiles (n=21). They were monitored for four foraging cycles (pre-switch, two days) to determine whether or not they crossed over to the other tile. On the fifth foraging cycle (switch, day three), one of the two tiles was switched with one of the three treatments-tiles with no mucus, self-mucus or mucus from a conspecific (other mucus). The number that crossed over to the treatment tile was calculated for foraging cycles six and seven (post-switch).

		Foraging cycle						
		Pre-switch				Switch	Post-switch	
Treatment	Crossed over?	(1	2	3	4)	(5)	(6	7)
No mucus	Yes	3	3	4	5	5	4	4
	No	4	4	3	2	2	3	3
Self-mucus	Yes	3	3	4	2	5	5	4
	No	4	4	3	5	2	2	3
Other mucus	Yes	6	6	5	4	7	4	4
	No	1	1	2	3	0	3	3

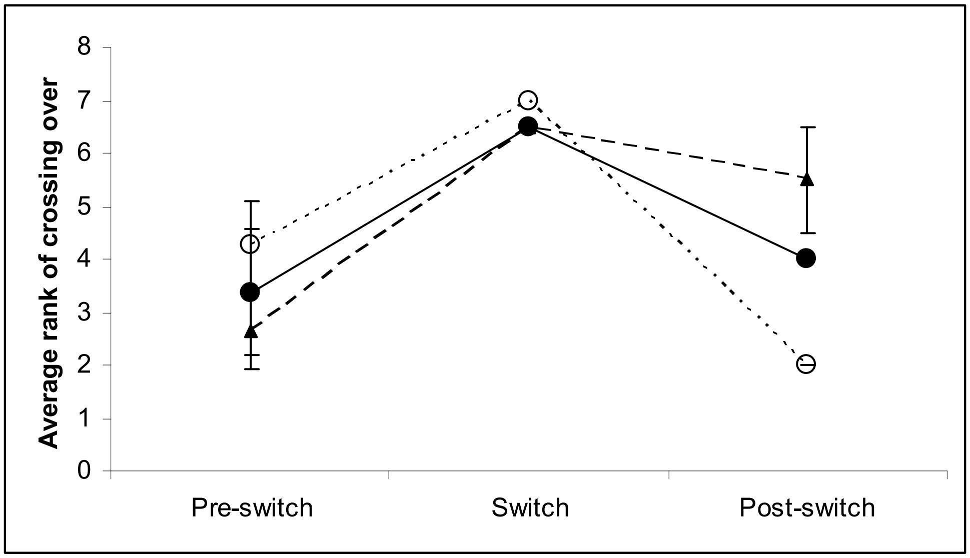


Figure 7.6. Two tile test without algae experiment. Average rank of individuals that crossed over to other tile (3 treatments, n=7 per treatment, 21 total) based on foraging cycle. Two foraging cycles occurred per day. Individuals were monitored for four foraging cycles (2 days) prior to the tile switch and the ratio of movers:non-movers was ranked and compared (2 way, non-parametric ANOVA, p=0.24). The ranks were averaged for pre-tile switch, tile switch and post-switch (average ± SE) for each treatment (no mucus = solid line, self-mucus = long dashed line, other mucus = short dashed line).

Discussion

Mucus serves many purposes, from aiding movement to promoting algal growth (Bretz & Dimock 1983, Connor & Quinn 1984, Davies et al. 1992a, Erlandsson & Kostylev 1995, Davies & Hawkins 1998, Hutchinson et al. 2007). I examined a potential new role of mucus, as a boundary marker in the territorial and homing limpet *Lottia gigantea*. Shanks (2002) reported that a territory holder prudently grazes in its territory, leaving ~71 % of the algal cover behind, compared to a non-territorial individual that leaves, on average, 50 % behind. *Lottia gigantea* do not necessarily avoid territorial borders, but may undergo a behavioral change in foraging when a border is encountered. Territory holders will graze prudently in their own territories, but when intruding on a conspecific's territory, they essentially clear-cut the area (A. Shanks, unpublished data). In the current experiments, I did not find evidence of enhanced residency on tiles belonging to a conspecific. In contrast, I found that *L. gigantea* avoided tiles marked with mucus from a conspecific, relative to tiles with their own mucus or neutral territory, that is tiles without any mucus.

The results from the 'territories with algae' experiment indicate that individuals preferentially visited tiles that were coated in self-mucus (their own territory) or no mucus (neutral territory) and visited tiles with a non-neighbor's mucus (marked territory) the least. Avoidance of marked territory tiles cannot be attributed to introduction of tiles into the arena because neutral territory tiles were also introduced into the arena and show enhanced residency relative to mucus treatments. This suggests that something on the tile, rather than simply a new tile, caused limpets to spend less time on the non-self mucus tiles. When *L. gigantea* encounters an invader in its territory, it shoves the interloper and chases it to the boundary of its territory (Stimson 1970, 1973, Wright 1982, Wright & Shanks 1993). The intruder quickly retreats to outside the territory. Avoidance behavior would assist the intruder by escaping costly encounters. Conversely, territory holders could avoid moving onto another individual's territory by sensing a conspecific's mucus. Territories of L. *gigantea* are often contiguous in the intertidal. By avoiding a conspecific's territory, an individual avoids potential costly encounters.

Another interesting aspect is that the two individuals in each arena did not form exclusive territories. Arenas were set up under the assumption that individuals would avoid each other and establish exclusive territories. As mentioned above, in the field individuals often form contiguous but exclusive territories (Stimson 1970). The original experimental plan was to switch tiles within arenas. It became apparent that individuals had not established exclusive territories so tiles from non-contiguous arenas were switched rather than within the arenas. In seven of the twelve arenas had enough overlap (overlap was > 2.5 tiles) to compare whether individuals visited tiles less frequently if the other individual visited the same tile. A correlation between the numbers of visits each individual made to shared tiles showed that there was not a negative relationship between how much time an individual spent on a tile based on the other individual's visits to the same tile for six of the seven arenas (Pearson's correlation, $p>0.05$ for all six correlations). One arena that had overlapping territories had a positive correlation (Pearson's correlation, $n=31$, $p>0.05$). Individuals visited tiles more frequently that the other individual had visited.

The algal biofilm was a variable, but since the tiles were evenly coated as confirmed with the chlorophyll samples, it was assumed that the algae did not add a confounding effect to the study. In the field there is an algal biofilm, so the presence of algae was biologically relevant. My second experiment examined the role of just mucus without algae present on the tiles. I demonstrated that a biofilm is a necessary interaction and cannot be teased out. There was no difference among the treatments and the only significant factor was time. After all the tiles were switched to their respective treatment tiles, the number of individuals that crossed over to the other tile increased**.** Whether or not the tile had mucus from another individual didn't seem to matter if no biofilm was involved. If food had been present, individuals that crossed over to tiles with no mucus or self-mucus may have stayed on that tile, while the individuals that crossed over to other mucus tiles would continue to avoid those tiles.

Mucus may serve as a chemosensory cue in territorial limpets. *Lottia gigantea* does not patrol its borders like other territorial animals, rather, it chases intruders when it encounters an interloper (pers. obs.). Mucus may be a way to communicate boundaries to conspecifics on a long term basis. By laying a mucus boundary on a substrate, an individual can avoid costly energetic confrontations. Scent marking is common in the animal world; theories to explain them range from scent marks being a possible sex attractant to a method of communicating information about age, dominance, etc. (Johnson 1973, Rich & Hurst 1998, Briscoe et al. 2002, Darden et al. 2008). Scent marking has been speculated to function in boundary marking around a territory (Peters & Mech 1975, Sliwa & Richardson 1998, Jordan et al. 2007, Kilshaw et al. 2009). While I focused on mucus as a chemosensory cue, the next step would be to determine how *L. gigantea* senses mucus and what components distinguish an individual's mucus from a conspecific's mucus.

CHAPTER VIII

GENERAL CONCLUSION

Lottia gigantea, the owl limpet, was used to look at general territorial questions and answer specific behavioral ecology questions about the organism. Before experiments were conducted, I had to establish the husbandry of *L. gigantea*. A combination of a constant food source and mimicking the natural tidal cycle contributed to my success in rearing *L. gigantea* in the laboratory. *Lottia gigantea* were maintained in good condition for eight months and new shell growth was evident with individuals growing an average of 0.9 mm/month during my preliminary study. The time-lapse system was also tested and individuals were tracked in the laboratory on a mock intertidal setup for seven days. All interactions of every individual were recorded.

A considerable amount of the work I did was based on models proposed by Stamps and Krishnan (1999, 2001). Stamps and Krishnan developed a new model of territory formation in which the experience of individuals dictates what locations they repeatedly visit and what locations they avoid. The authors suggested that affiliative experiences increase the likelihood that an animal will return to an area while agonistic experiences at a site will decrease the likelihood of their returning to that site. These assumptions are based on the initial stages of territory establishment when an organism is beginning to explore a novel area. Affiliative experiences can consist simply of a lack of agonistic encounters in a new habitat or an increase in habitat quality while agonistic experiences occur when two individuals interact and vie for space or food. In the first half of my dissertation, I examined the behavior of *L. gigantea* when they experienced affiliative situations. I tested the reactions of *L. gigantea* when they were subjected to agonistic experiences in the last half of my dissertation.

Once the techniques for husbandry and time-lapse system were established, I was able to examine how *L. gigantea* establish home ranges. *Lottia gigantea* appeared to explore the most during the first nine days of establishment. Individuals formed home scars within a week and established home ranges by the end of week four. Path length did not appear to determine home range size, but when path length and foraged area were scaled to body length, there was a positive regression; individuals that moved further distances had larger home ranges. The behavior of *L. gigantea* appears to fit one of the assumptions of the Stamps and Krishnan (1999) model: that an organism will return to areas where it does not experience agonistic encounters and favor familiar areas over novel ones.

It was assumed *L. gigantea* would return to areas with more food at a greater frequency than surrounding areas. To test this assumption, individuals were placed in arenas with varying algal density. Surprisingly, individuals avoided tiles with the most algae. Based on the time-lapse footage, it appeared that individuals grazed on the edges of algal dense tiles, but would not move over these tiles. I tested the hypothesis that individuals were avoiding these tiles because the tiles presented a danger, the danger being that they were too slippery. I placed individuals on tiles with varying algal densities and determined how much force it took to pull them off using a spring scale. It took considerably less force to pull individuals off tiles covered in algae. The foraging behavior of *Lottia gigantea* did not follow the Stamps and Krishnan assumption that individuals would favor areas with more food. Despite being a large food source, slippery rocks covered in algae posed more of a danger than a resource to limpets.

I then studied *Lottia gigantea* to see how they established territories in the presence of a conspecific competitor. Two similar-sized individuals were placed in an arena and monitored for 6 weeks using time-lapse photography. The number of interactions, the behavior expressed and the duration of each interaction were recorded. The degree of home range overlap was predicted to depend on the degree of aggression inflicted when the two newcomers meet. Aggression can range from minor (no damage inflicted) to escalated (serious injury or death frequently occurs). If the interaction is an escalated fight, the two individuals should have exclusive home ranges proportional to the amount of aggression inflicted by the individual, meaning that more aggressive individuals that win fights should have larger exclusive territories (Stamps & Krishnan 2001). If the interaction is less costly, then the two newcomers are more likely to have overlapping home ranges. The two main paired interactions demonstrated by *L. gigantea* were territorial / fleeing (one individual demonstrated territorial behavior and the other was evasive) and fleeing / bumping (one individual bumped into another and quickly fled while the other individual showed no reaction). Interactions occurred throughout the home ranges rather than at boundaries or near an individual's home scar, but there was a trend in that more interactions occurred inside the territories than at the boundaries. The degree of conflict appeared to be random as individuals had different reactions at the same location on different days. A limpet's overall behavior was independent of its neighbor's behavior; four of the seven dyads had two evasive individuals paired together. Despite the fact that over half the interactions had clear winners and losers, home range overlap (>75%) was considerable in six of the seven dyads even when one individual in the dyad was highly aggressive. Stamps and Krishnan (1999) suggest that individuals will avoid areas where they experience agonistic encounters, but only evasive *L. gigantea* had a tendency to decrease visits to areas where they had agonistic interactions. Territorial individuals avoided or returned to locations where they encountered another individual at the same rate.

To determine if individuals avoid areas where they experience agonistic losses, *L. gigantea* was subjected to repeated agonistic losses in the same location. *L. gigantea* were placed in individual arenas and their behaviors were followed for 7 weeks with time-lapse photography. *Lottia gigantea* established home ranges in the first 3 weeks and did not experience any agonistic encounters. After their home ranges were determined, territory holders were subjected to agonistic encounters where a territorial loss was mimicked on randomly selected tiles on the individual's home range periphery for two weeks. After 2 weeks the agonistic losses ceased and individuals were monitored for 2 more weeks. Their movements were scored to examine the probability of return to areas where they experienced agonistic losses. Visits to the agonistic loss areas were reduced, both during the training and after. *Lottia gigantea* appears to have learned behavior, as most individuals avoided the agonistic tiles during the training period. Home range area was similar before and after training, but individuals' areas were reduced during the agonistic training period. This suggests *L. gigantea* behavioral plasticity in its ability to determine present threats as it modified its home range area during the training period. *Lottia gigantea* follows the Stamps and Krishnan assumption that an organism will avoid an area where it experiences agonistic encounters but deviates from the model's prediction that an individual will expand its territory if additional space is available as individuals compressed the area they visited during the training period.

Lottia gigantea appear to distinguish between their mucus and a conspecific's mucus. Tiles with a conspecific's mucus were placed in arenas and individuals avoided these tiles. Individuals spent the least amount of time on tiles with conspecific mucus compared to both tiles without mucus and tiles with their own mucus, suggesting that there is a difference between self and non-self mucus. An experiment was conducted to determine how the presence of just mucus without an algal biofilm on a tile affected *L. gigantea*. Individuals were placed in arenas composed of two tiles on which there was no algal biofilm. Individuals were held in the areas for two days to ensure that the tiles had a mucus film. After two days, one of the tiles was switched to either a tile with no mucus or a tile with a conspecific's mucus. Individuals did not show any behavioral change when presented with a tile covered in a conspecific's mucus. This suggests the presence of algae (a food source) plays a role in how individuals react to mucus.

Over the course of five years, I was able to examine the behavioral ecology and territoriality of *Lottia gigantea*. While it demonstrates distinct territorial behavior, explaining its behavior is far from simple and requires further analysis. There was considerable variation found throughout my experiments which I believe to be a result of individual variation. My dissertation represents a foundation on which to build and further our knowledge about the behavior of *L. gigantea* and territoriality in general.

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Chapter VIII

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