

The establishment of a territory: effects of food and competitors on movement patterns in *Patella caerulea* limpets *

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Foragers which recruit or immigrate into a new area explore it, and thereby gradually establish a home-range or territory. We hypothesized that the rate of area acquisition is determined by the costs of movement relative to its benefits. To test this hypothesis, we explored the movement patterns of *Patella caerulea* limpets, transplanted onto panels in a fully crossed, replicated laboratory experiment. Experimental treatments were high and low food, high and low limpet density. The limpets gradually increased their home-ranges during the 14 days of experiment. In spite of only few observed aggressive encounters, the home ranges were largely exclusive, hence constitute territories. Territories increased faster at high than at low food densities. At low food densities territories increased faster with high than with low limpet density. Territory formation was slowest in low food-low limpet densities. We propose that the limpets mark territories with mucus trails. When food is abundant, the benefit of foraging is higher than the costs of locomotion and marking, favouring high movement rates and large territories. When food is scarce but competitors are many, limpet movement leads to marking rather than foraging, and they monopolize prospective resources by increasing their territories. When both food is scarce and competitors are few, the reward of either foraging or marking is low, making for slow territory-formation rates. Thus, prospective benefits are involved in the determination of territory-formation rates.

Previous studies proposed that the benefit of movement in low-food patches is acquisition of information on food distribution in changing environments. We suggest that an additional benefit lies in the exclusion of competitors for prospective resources.

KEY WORDS: density, foraging, limpet, marking, territory formation, territory quality.

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INTRODUCTION

An animal's movement pattern is eventually reflected in the size of its home-range. When the animal's trajectories are kept exclusive through active banishment of other individuals, the home-range is defined as a territory. When an individual migrates into a new area, or recruits to a population, it has to gradually establish its home-range through movement. It is likely that the extent of movement is determined by its benefits and costs, which depend on the animal's ecology.

For limpets, generalist intertidal grazers, the benefit associated with movement is energy acquisition through grazing. The cost of movement is made up of energetic expenditure for locomotion (DENNY 1980) and mucus production (DAVIES et al. 1990), predation risk (WELLS 1980) and the risk of detachment by waves (DENNY et al. 1983). In territorial limpets, additional movement is required for patrol and eviction of intruders.

We studied the development of movement pattern and the resulting home-range of the limpet *Patella caerulea* L. when introduced to a new area. Although navigation mechanisms in this species were explored (FUNKE 1968), the patterns of home-range formation or dynamics are not known. We hypothesized that the more food a newcomer encounters, the larger would be its benefit from movement and the faster would its home-range form. To test this hypothesis, we experimentally simulated two extreme types of surfaces in the laboratory: one containing food and one devoid of food.

Simulating an event of immigration, we transplanted limpets from the shore to these surfaces, and followed the development of their home-ranges by recording their movements. The establishment rate of the home-range may also be influenced by movement for territorial marking and protection. Such defensive behaviour is also more likely on high-food than in no-food surfaces, where territory protection has no immediate benefits. But it depends on the presence of prospective competitors as well. Therefore we used two densities of limpets on each type of surface. If territory-marking movement exists, we expected its level to be very low and independent of limpet density on no-food surfaces. On food-covered surfaces, we expected greater competition for food, and therefore more "territorial" movement, when limpet density is high than when it is low. The existence of "territorial" movement can, then, be inferred if differences in the extent of movement between density treatments occur only when food is supplied.

METHODS

Laboratory conditions

The experiments were conducted in a laboratory with constant fluorescent illumination and air temperature of 24 ± 2 °C. Limpets were kept in seawater aquaria, which contained at least 30 l at 22 ± 2 °C water temperature. The water was ventilated and filtered. Evaporated water was replaced with tap water every 2-3 days.

Experimental panels

The experiments were conducted on 30 × 30 cm plastic panels, on which a 1 × 1 cm grid was marked. Each panel was kept in a separate aquarium. The panels were hung horizontally, ca 2 cm below water level, and did not touch the aquarium walls so that the limpets could not escape.

Half of the panels were lined with slides carrying unicellular algae (see below), and were used to examine the limpets' behaviour under high food density. The remaining panels were lined with clean slides. These panels were scraped daily, without moving the limpets, to suppress algal development. They were used to observe behaviour under low food density.

Algae cultures

Unicellular marine algae were grown on clean microscope slides in Erdschreiber (MCLACHLAN 1973) algae growth medium. Growth was monitored through a weekly microscopic examination and chlorophyll determination (HANSMANN 1973). When a stable community dominated by a single species was achieved, the slides were glued to the experimental panels so as to form a continuous algal cover. This cover typically consisted mainly of unicellular red algae accompanied by bacterial film, unicellular green algae and diatoms. These algae were eaten by the limpets during the experiments.

Algal densities were estimated by chlorophyll determination of a sample of 2-3 slides from each panel. Sampled slides were replaced with algae-covered, ungrazed slides which had been kept in the same aquarium. Chlorophyll was also determined in a sample of the ungrazed slides in each aquarium, in order to estimate the relative effects of grazing and abiotic conditions on the algal populations. These samples were taken at the beginning of each experiment, a week afterwards and at its end.

Experimental animals

Young *P. caerulea* limpets (shell length 7-13 mm, adults are ca 30 mm) were used, since they are more likely than adult limpets to encounter circumstances under which they have to establish a new territory. The limpets were collected on the Ashdod beach (31°50'N-34°39'E, Mediterranean Sea) in the winter of 1991 and brought to the laboratory within a few hours of collection. Before the experiments, limpets were housed on plastic panels which were hung horizontally in the aquaria or laid on their floor, and acclimatized for at least a week to laboratory conditions. They fed on algae which developed on these panels.

Experimental animals were individually marked and placed at the desired densities on the panels, facing away from the observer. Their initial locations were determined by using a random number table.

Experimental design

A total of 20 limpets were arbitrarily allocated to each of 6 panels (3 high-food replicates and 3 low-food replicates). To each of 18 additional panels (9 with high food, 9 with low food) 3 limpets were allocated. Thus, four treatments were administered: high limpet density with either high or low food density (60 limpets in each treatment), low limpet density with high or low food (27 limpets in each treatment). The coordinates and orientation of all limpets were recorded in hourly observations during the first 14 days of each experiment, between 10 a.m. and 2 p.m. Movement, interactions and other events were also recorded during each observation.

Video filming for movement tracking

A total of 111 limpets were video-filmed in the laboratory for periods of 3-24 hr each (totaling 105 filming hours), after a week or more of acclimatization to laboratory conditions. The camera was placed above an aquarium which was arranged similarly to the experiment aquaria. The films were analyzed for close tracking of the limpets' trajectories, movement periods and speeds.

Data analysis

Consecutive coordinates at which each limpet was observed were connected by straight lines, which made up the individual's path. The underlying assumptions were that limpets used the shortest possible path between points of observation; and, that limpets which occupied the same location at consecutive observations had not moved between these observations.

The analysis included only individuals which took part in the whole experiment. The data for each day were analyzed separately. For each limpet, the output of the analyses included:

1. A map which included the locations in which the individual was observed, and the presumed paths connecting among them.
2. An estimate of the home-range size, which was defined as total trajectory length multiplied by mean trajectory width (which was 1 cm). In vertebrates, home-range sizes are commonly estimated through computation of the areas which are bound by the points where individuals were observed (e.g. FORD & KRUMME 1979). These algorithms are valuable when the number of observations is small; and, when it can be safely assumed that an individual which is observed at several peripheral locations also exploits the area bounded by them. As these conditions do not apply to our experiment, we consider trajectory area a more accurate estimate of home-range size.
3. An estimate of the fraction of trajectory area which had been previously visited by the individual. This was used as an index of the limpets' fidelity to their home-ranges.
4. An estimate of the overlap level with the home-ranges of each of the other limpets on the same panel throughout the whole experiment. This estimate is the average of overlapping trajectory area for every combination of two limpets on a panel, weighted by the total cumulative movement of these individuals.
5. The frequency of movement, expressed as frequency of location change between consecutive observations.
6. The frequency distribution of trajectory lengths.

The relative effects of food density and limpet density on home-range sizes were determined through one- and two-way ANOVA. Forage density was treated as a discrete variable with two possible values ("high" and "low"). The establishment rates of the home-ranges were estimated by linear regression of home-range size on time. Discrete distributions were compared through G-tests. SAS-PC version 6.03 software (SAS INSTITUTE 1988) was used for analyses.

Since the limpets' behaviour was not uniform throughout the experiments, time can be considered an additional independent variable. However, as behaviour on one day may influence that on the next, only data which were collected on the same day of experiment in the various treatments were compared.

RESULTS

Food available to the limpets

The amounts of algae in the high-food treatment varied widely among sampled slides and among panels (Table 1). In the no-forage treatment, a low level of algae was maintained. A decrease in algal biomass is evident in the high-density treatments during the second half of the experiment. A more moderate decrease also occurred in the ungrazed slides. This decrease may result from poor light and nutrient conditions in the experimental aquaria as compared to the algal growth medium. It suggests that, although foraging significantly affected algal densities (one-way ANOVA, $F_{50} = 20.27$, $P < 0.001$, $R^2 = 0.29$), it was not the only important factor. The effect of foraging on algal biomass in low-density treatments was also highly significant, but smaller (one-way ANOVA, $F_{150} = 29.35$, $P < 0.001$, $R^2 = 0.16$).

In spite of grazing and scraping of the panels, algae were not completely eliminated in the low-forage treatments. Possible explanations are settlement of suspended algae, perhaps their trapping in the limpets' mucous trails, or accelerated algal growth on the mucus (CONNOR 1986).

Home-range sizes

The mean trajectory and length of a movement bout were 23 cm and 52 min, respectively, yielding a movement speed of 0.52 cm/min. Average movement during the daily period of observations ranged between 4 and 21 cm. A steady increase in cumulative home-range size resulted from this movement (Fig. 1). Inter-panel differences in the extent of movement within each experimental treatment were not significant. Therefore movement data of all limpets within a treatment could be pooled for statistical analysis.

In order to compare the rates of home-range expansion among treatments, we plotted cumulative home range sizes vs time for each treatment and fitted a linear

Table 1.
The effect of the limpets on algal biomass, expressed in mean (\pm SD) chlorophyll ($\mu\text{g}/\text{cm}^2$).

Food density	Limpet density (no. per panel)	Initial	Chlorophyll concentration	
			after 1 week	after 2 weeks
Low	Low (3)	0.0	3.6 \pm 2.1	1.3 \pm 1.6
	High (20)	0.0	7.8 \pm 3.3	0.5 \pm 0.6
High	Low (3)	56.5 \pm 29.3	41.2 \pm 19.9	48.3 \pm 29.4
	High (20)	23.5 \pm 21.8	24.4 \pm 10.4	5.5 \pm 2.8

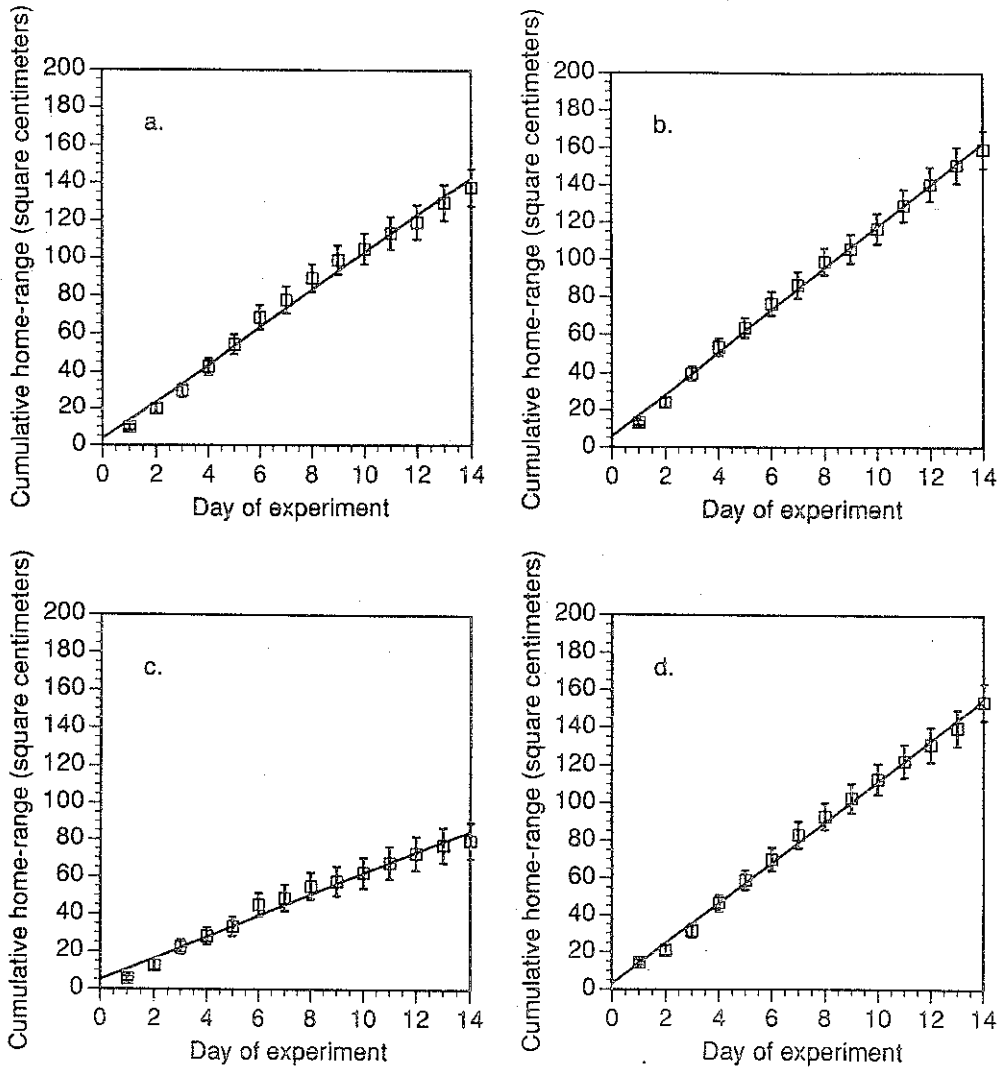


Fig. 1. — Mean (\pm SE) cumulative home-range sizes. Data of all limpets in each treatment were used for computation of the regression lines. (a) No food supplied, 20 limpets per panel; regression equation is $Y = 9.94X + 3.68$, $R^2 = 0.37$, $P < 0.001$, SE for regression coefficient = 0.47. (b) Food supplied, 20 limpets per panel; regression equation is $Y = 11.20X + 5.84$, $R^2 = 0.44$, $P < 0.001$, SE for regression coefficient = 0.44. (c) No food supplied, 3 limpets per panel; regression equation is $Y = 5.70X + 5.16$, $R^2 = 0.27$, $P < 0.001$, SE for regression coefficient = 0.50. (d) Food supplied, 3 limpets per panel; regression equation is $Y = 10.94X + 2.88$, $R^2 = 0.39$, $P < 0.001$, SE for regression coefficient = 0.47.

regression. The slopes of the regressions were compared using F-tests (Table 2). The rate of increase was highest in the two high-food treatments, lower in the high-density no-food treatment and lower still in the low-density no-food limpets (Fig. 1).

The experimental variables — food and limpet densities — significantly ($P < 0.05$) affected home-range sizes from day 4 of the experiment onward (Table 3). Their effect increased with time, from 6% of the variation explained on day 4 to 14% explained on day 14. While food density had a significant effect on 12 out of 14 days, the effect of limpet density became significant only after 8 days and their interaction was significant only on day 14.

Overlap and exclusivity

A certain proportion of the limpets' daily trajectories overlapped trajectories of previous days. Only the remaining movement, which occurred in new areas, led to increases in the limpets' home-range. Although home-ranges increased with time and their cumulative area did not level off, the fraction of "new" paths out of the daily movement decreased with time as the experiment progressed. The fraction of "old" paths increased accordingly (Table 4, "observed" values). If visits in "old" areas are neither preferred or avoided, nor dictated by the geometry of the home range, their frequency should be proportional to the fraction of panel area which has already been visited (Table 4, "expected" values). The high rate of recurring visits suggests that "old" areas were preferred or that "new" areas were avoided.

The levels of exclusivity in area use were estimated by pairwise comparisons between each limpet's path and those of all other individuals on the same panel. The fraction of overlap between any two such paths was averaged over all limpet pairs on

Table 2.

Rates of home-range expansion within the 14 days of the experiment. Cumulative home-ranges were plotted against time for all limpets in each experimental treatment. Linear regression lines were fitted to the plots (Fig. 1). F-values are from pairwise comparisons between the regression slopes. The slopes express the relative rates of home-range expansion.

Treatments compared	Slope	F-value	df
High density, no food - high density, high food	9.94 11.20	7.38 **	769
Low density, no food - low density, high food	5.70 10.94	111.64 ***	349
High density, high food - low density, high food	11.20 10.94	0.37 NS	825
High density, no food - low density, no food	9.94 5.70	82.64 ***	769
High density, no food - low density, high food	9.94 10.94	4.57 *	769
Low density, no food - high density, high food	5.70 11.20	159.76 ***	825

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

Table 3.

The effects of food and limpet densities on cumulative home-range sizes, analyzed through 2-way ANOVAs.

Day of experiment	F-value for effect of				Fraction of variation explained
	Complete model	Food	Density	Interaction	
1	2.44 NS	6.39 *	0.61 NS	1.12 NS	0.04
2	1.73 NS	2.94 NS	1.94 NS	0.29 NS	0.03
3	2.28 NS	3.43 NS	2.22 NS	0.01 NS	0.04
4	3.28 *	6.26 *	2.79 NS	0.50 NS	0.06
5	3.44 *	6.25 *	3.33 NS	1.36 NS	0.06
6	2.91 *	5.21 *	2.79 NS	1.63 NS	0.05
7	3.40 *	5.79 *	3.50 NS	2.00 NS	0.06
8	4.11 *	6.16 *	5.09 *	2.05 NS	0.07
9	4.67 **	7.00 *	5.16 *	3.78 NS	0.08
10	5.16 **	8.86 **	5.13 *	3.34 NS	0.09
11	5.95 ***	11.03 ***	5.33 *	3.47 NS	0.10
12	6.69 ***	13.71 ***	4.96 *	3.31 NS	0.11
13	7.04 ***	12.46 ***	7.09 **	3.00 NS	0.12
14	8.17 ***	15.82 ***	6.7 *	4.83 *	0.14

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$, $df = 159-160$ for all analyses.

Table 4.

Mean (\pm SD) proportions of revisited areas on days 2, 7 and 14 of the experiment-observed and expected values. The relationship $\text{area foraged/total panel area} = \text{revisited area/area foraged}$ is expected if recurring visits are neither preferred nor avoided, and was used to compute the expected values. Observed values were always significantly higher than expected values ($P < 0.001$, G-tests for goodness of fit, $df = 1$), except when marked by *, where the test could not be performed because $df = 0$.

		Day of experiment		
		2	7	14
Low forage	Obs	0.47 \pm 0.41	0.56 \pm 0.34	0.64 \pm 0.34
High density	Exp	0.02 \pm 0.02	0.09 \pm 0.06	0.15 \pm 0.08
High forage	Obs	0.37 \pm 0.39	0.54 \pm 0.36	0.63 \pm 0.38
High density	Exp	0.03 \pm 0.03	0.10 \pm 0.05	0.18 \pm 0.08
Low forage	Obs	0.36 \pm 0.53	0.63 \pm 0.38	0.81 \pm 0.31
Low density	Exp	0.01 \pm 0.01	0.05 \pm 0.04	0.09 \pm 0.06 *
High forage	Obs	0.47 \pm 0.38	0.41 \pm 0.38	0.42 \pm 0.38
Low density	Exp	0.01 \pm 0.01 *	0.09 \pm 0.06	0.16 \pm 0.10

each experimental panel and served as an index of exclusivity. This index may range between 0, when paths are completely exclusive, and 1, indicating completely overlapping paths. The exclusivity index averaged between 0.05 and 0.08 for the four experimental treatments, which means that foraging paths were largely exclusive.

Encounters and aggression

In accordance with the exclusivity of home-ranges, encounters among limpets were rarely observed: of 12,090 point-time observations, in only 18 (i.e. 0.15%) a contact between two limpets was observed (13 in the high density, no food treatment, 5 in the high density, high food treatment). Only one of these contacts — in the no-food group — elicited apparent aggression. But the occurrence of 11 aggressive interactions during the 120 video-filmed movement bouts suggests higher rates of aggression.

DISCUSSION

Competitor density in low-food treatments and food density in low-competitor density treatments significantly affected the limpets' rate of home-range expansion: expansion rates were highest when food was high, lower in the low-food, high-density treatment and lower still in the low-food, low-density treatment. The ANOVA interaction between food and competitor densities was low, and we therefore propose that home-range formation rates are independently influenced by food and competitor densities. The behavioural differences between high-density and low-density limpets in low-food treatments indicate that they received some information on their competitor number in spite of the daily scraping of the panels.

Home-ranges increased faster, and were larger in the high-food treatments than in the low-food treatments, thus supporting our first hypothesis that limpets benefit from movement when food is abundant more than when it is scarce. An alternative explanation in the framework of the cost-benefit model is that the cost of foraging is lower in high-food areas than in low-food areas. However, food consumption, growth rates and gonadal weight were higher in *Patella vulgata* L. from a rich site than in a population from a site of low primary productivity (WORKMAN 1983). This indicates that limpets forage as energy maximizers (SCHOENER 1971, HIXON 1982), namely that intensive foraging, when food is plentiful, is rewarding.

The effect of competitor densities on home-range formation rates depended on the food density. When food densities were high, there was no clear effect of limpet densities. Under low food densities, home ranges increased faster when competitors were many than when they were few. Our second hypothesis, that the extent of potential "territorial" movement would be affected by limpet densities on high-food surfaces only, therefore requires modification.

High competitor density may increase the benefits of movement in two ways:

a) Limpets may obtain information on the spatial distribution of food by moving and sampling various feeding sites (BELL 1991). If high competitor density increases the spatial variability of food sources, then movement will yield information on the environment, which cannot be obtained by sampling the immediate surroundings. Thus, high movement and sampling levels may be favoured when forager density is high because food patchiness is increased. Since home-range sizes were not affected by limpet density in the high-food treatments, this explanation is not likely.

b) If chemically marked areas tend to be avoided by other foraging limpets, then marking during locomotion may reduce the exploitation of the marked area by other limpets. Food which may eventually arrive at such areas would be mainly harvested by the marking individual. In low-food treatments, the immediate bene-

fits of "territorial" movement may be low, as we initially assumed; but when the density of potential competitors is high, the expected future benefits of territorial marking may be high enough to make it worthwhile.

According to this hypothesis, apart from foraging, the function of locomotion is monopolization of potential resources by non-aggressive territoriality. This is supported by the observed limpets' high site tenacity and low site overlap, indicating that large parts of *P. caerulea*'s home range are exclusive, and that the population is largely territorial. Mucus trails of three species of limpets persisted in the laboratory for 11-19 days (CONNOR 1986). Thus, a low marking frequency may suffice to create a fairly high exclusivity in home-range use.

An increase in competitor density may decrease food density and, hence, reduce the benefits of locomotion. Such a reduction would be very marked if limpets reacted immediately to changes in food availability. If so, the increasing divergence in food availabilities among panels, as the experiment progressed, should have led to large differences among panels in the limpets' extent of movement. However, there were no significant differences in locomotion rates among limpets from different panels. This suggests that the behavioural reaction to changes in food availability was slow. If, on the other hand, limpets avoid areas marked by their competitors (possibly after some aggressive interactions), an increase in competitor density would increase the benefit of movement for marking purposes. Increased movement, leading to larger territories would then be expected.

We suggest that the benefit of movement is both in foraging for food and in securing its acquisition through territorial marking. The cost consists of energetic expenditure for locomotion, predation risk and the risk of being swept by waves. Our experiment indicates that the benefit of high food density is greater than the cost of locomotion for both foraging and marking, favouring high movement rate and large territories. However, when many prospective competitors are around, it pays a limpet to secure future resources by somewhat enlarging its territory even if current food density is low. When both food density and number of competitors are low, the reward of either foraging or marking is low, and it becomes advantageous to reduce movements and hence not to increase the existing territory. Thus, cost-benefit considerations may affect the rate of territory acquisition (Fig. 2).

Although territory sizes did not stabilize during our 2-week experiment, we tried to apply our results for extending DAVIES & HOUSTON's (1984) conceptual model of optimal territory size (Fig. 3). This prediction rests on the yet untested assumption, that territory formation rates are correlated with territory sizes, when they eventually stabilize.

Fig. 3 predicts that territories at equilibrium will be smaller when competitors and food are scarce than when one of them, or both, are abundant. But field studies do not support the prediction: in several vertebrates (e.g. MYERS et al. 1979, HIXON et al. 1983, TRICAS 1989, ENOKSSON 1990, JONES 1990), and invertebrates (HART 1987), including limpets (STIMSON 1973), feeding territory sizes were inversely related to the amount of food they contained. CARPENTER (1987), MYERS et al. (1979) and TRICAS (1989) showed that food-rich territories are smaller than poor ones because, at least in some cases, they attract more competitors and thus are harder to defend. The model for optimal territory size may be improved if this cost component is quantified and incorporated.

To conclude, we propose that not only the immediate benefits, but also future rewards, affect the limpets' rate of locomotion and territory acquisition. STAMPS &

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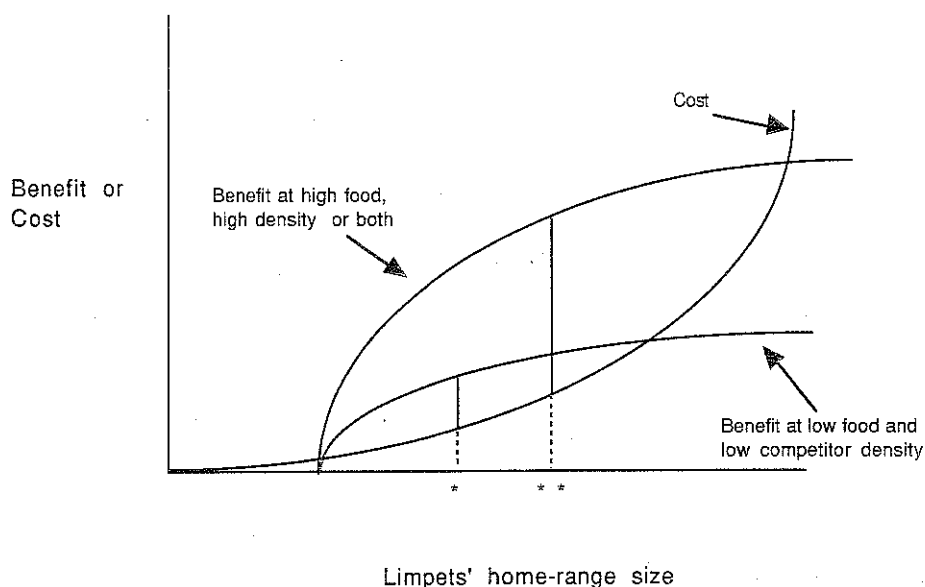


Fig. 3. — Proposed extension of DAVIES & HOUSTON's (1984) conceptual model to optimal equilibrium home-range size in limpets: when home-range size is optimal, the difference between the benefit and cost of its maintenance is maximized. At high food density or limpet density, the immediate or expected amount of energy (benefit curve) obtained per unit area foraged is higher than when food is scarce and competitors are few. This leads to smaller optimal home-range sizes under low-food, low-density conditions (*), vs larger optimal home-range size under high-food or high-density conditions (**).

food densities, the expected future benefit of movement, and of territory expansion, is twofold: (i) the acquisition of information on the abundance of the time-variable resource, and (ii) the exclusion of potential competitors.

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