A Mechanism for Passive Range Exclusion: Evidence from the European Badger (*Meles meles*)

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The Passive Range Exclusion (PRE) Hypothesis provides a mechanism whereby species that rest or breed in communal residences, but forage independently on dispersed food items, may avoid entering the core home ranges of neighbouring groups. A stochastic simulation shows that as the occupants of a communal residence travel outwards to feed, their activities create a gradient in food availability. Food closest to the point of origin tends to be discovered first and at the highest rate. As the foraging period continues, the probability of encountering unexploited food increases with distance from the residence. Areas of relatively high food availability persist as ridges between neighbouring communal residences. The simulation predicts that once such a gradient is established, a strategy of preferential feeding in these areas optimizes food intake. Feeding excursions deep into neighbouring ranges are disadvantageous because areas of lower food availability are encountered and travel times back to the home residence become longer. The observed reluctance of individuals to forage close to neighbouring residences can therefore be explained partly or wholly as a result of exploitation competition and feeding optimization, without necessarily invoking territorial arguments about interference competition and conflict avoidance.

At lower forager and food patch densities the simulation indicates that the gradient is insufficient to award significant benefit to border feeding. Hence border feeding strategies and the range exclusion that results should diminish as food or forager densities decrease. We use the European badger (*Meles meles* L.) as a test case for the hypothesis and show that exploitation competition between groups may be an important factor in shaping this species' home ranges.

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Introduction

ACTIVE DEFENCE AND INTERFERENCE COMPETITION

Many group living species apparently exclude neighbouring groups from a core feeding range. The mechanism of this exclusion is often assumed to be active defence of the contested area. The function of this active defence is to gain privileged access to resources that are in some way limiting. Active defence is favoured when the fitness costs of defence are smaller than the fitness benefits of monopol-

ization. Active defence can take several forms. In interference formulations, stable occupation of an exclusive home range indicates the existence of a contest asymmetry that has favoured the owner over previous challenging intruders. This contest asymmetry can be a difference in resource holding potential (Parker, 1974), an owner/intruder pay-off asymmetry (Ydenberg *et al*., 1986), or an established ownership convention (Davies, 1978b). It predictably allows or encourages the resident to escalate conflict above the level at which it is profitable for the challenger to continue. Such exclusive ranges can be maintained with only the threat of overt aggression, providing the intruder and owner are aware of the contest asymmetry. Such awareness can be achieved through

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honest signalling, testing willingness to escalate, or perception of a pay-off asymmetry. Another less well documented class of active defence can occur through resource exploitation. Patterns of foraging are modified so that food is not lost to intruding neighbours (Paton & Carpenter, 1984) or so that a perimeter area of resource depletion discourages neighbours from crossing into a core area (Peres, 1989). This is active defence in so far as the strategy of range use is costly because it does not optimize short-term foraging success, but has evolved instead to impede intrusion by others and bring long-term fitness benefits.

Active defence is the commonest criteria for conceptual definitions of *territoriality*. Hence Maher & Lott (1995), after an extensive review of the literature, suggest the definition of territory as "a fixed space from which an individual or group of mutually tolerant individuals, *actively excludes* competitors for a specific resource or resources". An operational definition of territory will therefore include some measure of range overlap and defensive behaviour for the species concerned.

PASSIVE DEFENCE AND EXPLOITATION COMPETITION

Authors such as Kaufmann (1983) and Davies (1978a) have asserted that mutual avoidance can create range exclusion without active defence. The suggested cause of mutual avoidance in this non-territorial formulation is generally avoidance of exploitation competition. We refer to this as passive range exclusion or PRE. Very few studies have demonstrated the effect. Alatalo *et al*. (1987) showed socially subordinate tit species, apparently incapable of interference competition, restricted the feeding activities of the larger more socially dominant species by exploitation competition. Davies & Houston (1981) showed for the Pied Wagtail (*Motacilla alba*) that while range exclusion was maintained by active defence of positions just ahead of the bird's circular foraging path, range exclusion was maintained behind it by exploitation competition. They coined the term "defence by depletion" for this type of PRE, and Davies (1981) suggested that it was why intruders retreated as soon as ownership was announced as the presence of an owner signalled unprofitable foraging for others.

In this paper we use a stochastic simulation to show how exploitation competition can influence foraging success and hence foraging strategy in group living species. We hypothesize that defence by depletion can be a sufficient explanation for PRE between contiguous neighbouring groups, and so help determine the size and shape of home ranges for

group living species that fulfill certain criteria. We argue that the importance of this simple mechanism is overlooked for even well studied species because it can exist side by side with, or even reinforce, active defensive strategies.

The Simulation Model

INTRODUCTION

A stochastic computer simulation model (probabilistic cellular automaton) was written in "C" on a Digital UNIX 3.2c system. Its role was to examine the effects of exploitation competition without interference competition for group living central place foragers. We developed the simulation to mirror the spatial system of the European badger (*Meles meles*) in lowland England, but intend it to be generalizable to other species such as communally roosting insectivorous bats, or lagomorphs grazing from shared warrens. The simulation is performed on a board of hexagonal cells. It is divided into seven identical hexagonal ranges, a central range surrounded by the other six in a hexagonally close-packed arrangement (see Fig. 1). The centre of each range contains a cell designated as the "residence". The size of the ranges is determined by the parameter b, the number of bands surrounding the residence, that is, "annuli" of cells at the same distance from the residence. A number, f, of food
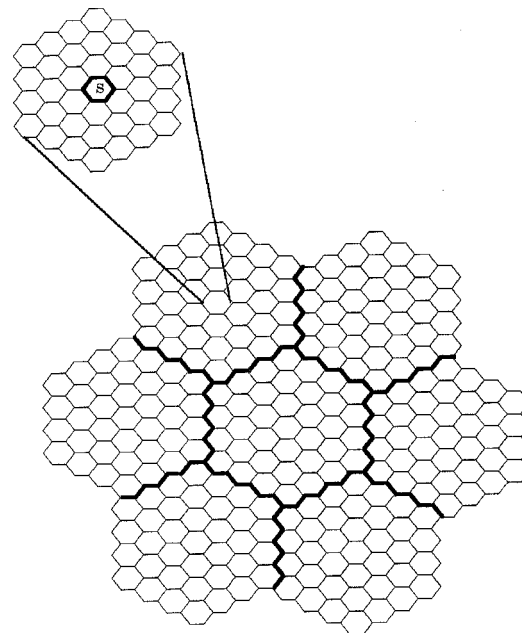

FIG. 1. A diagrammatic representation of the board and its seven home ranges. In this case, the size of each group's range is just 24 bands, three directly around a residence (shown by an "s") and 7 bands (not shown) in each of the three larger hexagons.

points are assigned to each cell of the board independently with a probability p, using a uniform distribution, $U(0,1)$.

A group of g players (analogous to foragers) emerge from each residence at the start of a round of m moves (analogous to one foraging period, e.g. a night's foraging). Whilst foraging, players move simultaneously to adjacent cells of the board. If they land on a cell containing food, then they are delayed for a handling time of h moves whilst consuming the food. The food is shared between those players that simultaneously discovered the cell and is made unavailable to any other players landing on that cell in subsequent moves. Players continue to forage on the board until there are only enough moves to take them back to their residence by the shortest possible route.

A "boundary" is defined as the dividing line between the two bands of cells equidistant between residences. The "home range" is the series of cells within the boundary. Players in the centre residence can play two strategies. A "free-roaming" strategy where their movement is unrestricted over all of the seven home ranges (with the exception of entering any of the residences), or a "boundary mover" strategy where movement is restricted to one band either side of the boundary once they have reached it. The players in the outer six ranges can play either a free roaming or "territorial" strategy (determined by the test conducted). With a territorial strategy movement over the board is confined to the cells of their home range.

A trial consists of a cumulative total of each individual's score from a series of previous foraging periods.

SIMULATION ASSUMPTIONS

Territories and groups

(1) All seven territories are equal in all properties, i.e. size, shape, proportion of cells that contain food and the amount of food that may be contained on a cell.
(2) All groups contain the same number of players.
(3) Each foraging period of a trial contains the same number of moves.
(4) Where a trial contains more than one foraging period, the score of each player is carried over to the next period each time.

Movement and strategies

(1) All players move simultaneously, the movement of one player does not affect those of another.

(2) Players may not move in the direction from which they have just travelled except on the first move of their return.
(3) All players within a group play the same strategy.
(4) A player plays the same strategy during each move of each foraging period during a trial.

Food and feeding

(1) Each cell is independently assigned food using a uniform distribution $U(0,1)$. That is, if $U(0,1) < p$ then food is assigned to that cell.
(2) At the start of a foraging period, a cell either contains f or zero food points.
(3) If a player(s) land(s) on a cell containing food that is available for feeding upon:
  (i) the food is then unavailable to any other players that may land upon that cell in subsequent moves of the foraging period;
  (ii) the food is shared equally between all of the players that simultaneously landed on that cell;
  (iii) the food is shared out equally over handling time moves.
The players remain on that cell for either:
(a) handling time moves or
(b) until they are forced to return home. That is, if x players land on a cell containing y food points and handling time is z moves, each receives y/xz points on each of z moves.

Returning

(1) Each player continues to forage until it is forced to return home.
(2) A player is forced to return home when its distance in cells from its home residence is one less than the number of moves left in the foraging period.
(3) When returning home, players may not feed upon any food that they land upon (because the handling time would cause the foraging period to exceed the permitted number of moves).
(4) All players return to their group's residence.
(5) All players return by the shortest possible route.

Results from Simulation

Hereafter, 'F' denotes the test/statistic from an F distribution test and 'n', number of replicates.

ESTABLISHMENT OF GRADIENT

Figure 2(a) shows the establishment of a food density gradient at ten-move intervals, over the
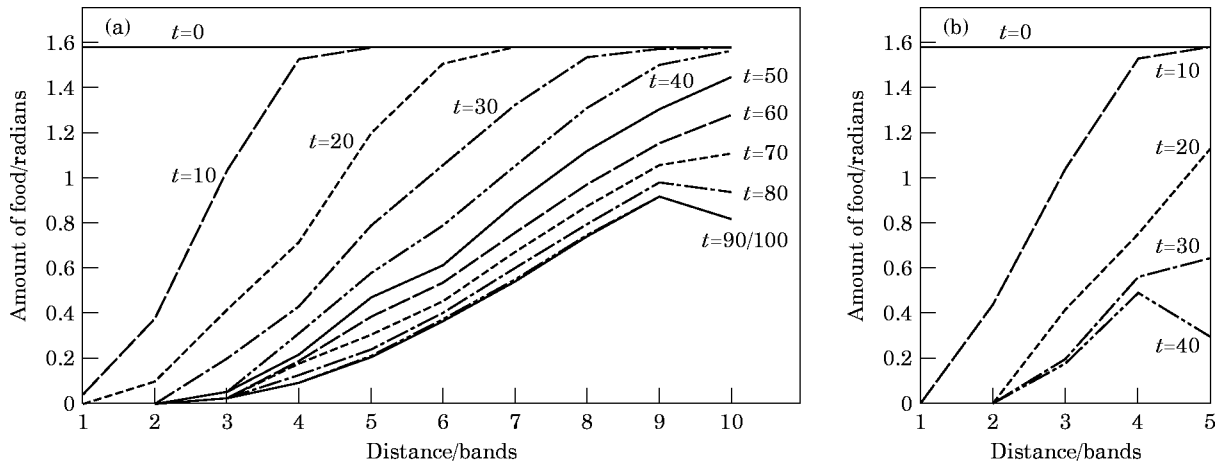
FIG. 2. The establishment of a food density gradient at ten move intervals in a home range of size (a) bands = 10 and (b) bands = 5 with the central group employing the "boundary mover" strategy. The size of all groups was 20.

central range, during the course of a foraging period averaged from ten rounds. Central group members employed a boundary mover strategy whilst those of the outer groups employed a territorial one. A similar figure is obtained for the situation where all group members play free-roamer and can thus "invade" the central group's range. Food nearer the residence is more depleted, and depleted earlier, than food at greater distances and the profiles are sigmoidal up until the point where the first players have reached the boundary ($t > 30$) and start to "eat into", and reduce, the gradient. Figure 3, charts the establishment of this gradient ($t = 0$ until first arrow), the depletion of the gradient as it is exploited (period between first and second arrows) and a static gradient as the players are forced to return home and thus cannot forage. As boundary movers are essentially employing the same rules as territorial players until they reach the boundary corridor, a similar profile extends from the
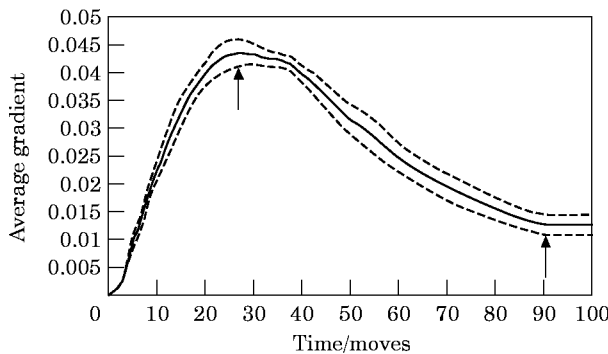

FIG. 3. The average gradient during one night's foraging ($n = 10$). The gradient is established in the period up to the first arrow when the first players have reached the boundary. They then exploit this gradient up until the second arrow when the last player is forced to return home and the food distribution, and consequently the gradient, becomes static. The dashed lines show the 95% confidence intervals.

neighbouring residence. Thus we can imagine the profiles as symmetric ridges between the two residences. Figure 2(b) shows the situation when the inter-residence distance is halved to 5. Players reach the boundary earlier in the foraging period and the ridges formed are sharper. We conclude that the foraging activities of neighbouring groups create a predictable pattern of resource availability. It results in ridges of relatively high food density mid-way between residences of equal size even after players have reached the boundary.

ADVANTAGE OF FEEDING AT BOUNDARY REGION

Table 1 shows the results of linear regressions between the food point scores and the amount of time spent foraging within the boundary region at a variety of food densities. Twenty-five trials of teams of 20 were simulated. Only players that spent one or more moves in the boundary region have been included in the analysis. Above a food density of 0.02 there were highly significant relationships between the scores obtained and the amount of time spent in the boundary region. The total number of moves was set at 100 and thus it is appropriate to think in terms of the proportion of the foraging trip spent in the boundary region. There is an advantage to foraging preferentially at the boundary region. Further, there is a positive relationship between the regression gradients and food density (F = 72.9, $n = 13$, $P < 0.0001$) showing that this advantage increases with food density. This result arose because there was a highly significant relationship between the maximal gradient established within a foraging period and food density (F = 842, $n = 101$, $P < 0.0001$: Fig. 4).

We conclude that there is an advantage to players pursuing a preferential border-feeding strategy. The

Food density	Regression intercept	Regression gradient	n	F	Significance
0.01	31.3	0.0863	421	2.69	N.S. $(P < 0.01)$
0.02	74.3	0.49	419	0.38	N.S. $(P < 0.05)$
0.03	79.3	3.05	423	12.63	***
0.04	101	3.81	428	13.88	***
0.05	115	4.96	423	22.47	***
0.10	219	10.9	421	56.37	***
0.20	527	17.1	409	62.04	***
0.30	717	23.2	407	88.40	***
0.40	995	22.8	384	63.28	***
0.50	1235	29.1	386	78.21	***
0.60	1455	34.1	355	80.11	***
0.70	1759	31.4	363	74.58	***
0.80	1830	40.1	334	99.17	***
0.90	2102	38.9	318	95.31	***
1.00	2385	32.4	307	50.10	***

$*** = P < 0.0001$.

The results of linear regressions between the food scores (dependent variable) and the number of moves within the boundary region (independent variable) for various food densities. Parameters: bands = 10, moves = 100, team size = 20, food value = 200, handling time = 4 and boundary size = 1.

advantage is greatest with high initial food patch density.

EFFECT OF GROUP SIZE

Table 2 shows a comparison between the average gradient established during the course of a foraging period for a single forager against that of a group of 20. The single forager creates a far smaller gradient, and thus there is only a small advantage to border foraging. There was a highly significant positive relationship (F = 466, $n = 50$, $P < 0.0001$) between the maximal gradient established within a foraging period against the $\log_e$(group size), see Fig. 5. As groups become larger the increase in the gradient produced per additional individual decreases. We conclude that the PRE effect is most marked for group living species that forage separately.
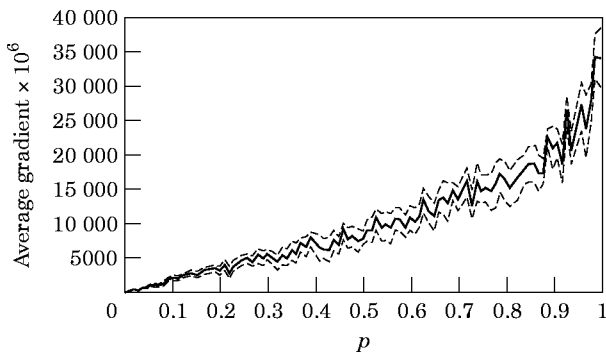

FIG. 4. The relationship between average gradient ($n = 10$) and food density. The dashed lines show the 95% confidence intervals.

EFFECT OF INTRA-GROUP COMPETITION REDUCTION

Competition between members of the central group was reduced by sequentially allocating each group member one of six directions and then giving them stochastic directional fidelity. This produced a highly significant increase in their scores (t-tests with pooled variances, $2.68 \le t \le 29.9$, $P < 0.0001$) at all non-zero food densities. We conclude that intra-group exploitation competition has an effect that can be reduced by simulating avoidance of other forager's sectors.

SUMMARY OF RESULTS

(1) A food density gradient is established during a foraging period as food closer to the residence is found earlier and at a higher rate than food further away.

(2) As the inter-residence distances decreases, so the "ridges" that represent under-utilized foraging zones become more sharp and the greater the "penalty" of veering away from the ridge crest whilst foraging.

(3) The larger the proportion of the foraging trip that is spent at the boundary, the higher is the player's score and this differential increases with increasing food density.

(4) The larger the group size, the greater is the food density depletion gradient and the greater the advantage to feeding at the boundary.

(5) Reducing intra-group competition by simulating avoidance amongst the players significantly increases their scores.

TABLE 2

The average gradient (and standard deviation, S.D.) created during the foraging period for a single forager and a group size of 20

	Single forager		20 foragers	
Time	Gradient $\times 10^5$	S.D. $\times 10^5$	Gradient $\times 10^5$	S.D. $\times 10^5$
10	164	16.1	2276	246.3
20	320	34.9	3978	293.2
30	454	109.7	4348	259.3
40	548	186.2	3985	224.0
50	606	228.1	3174	384.2
60	671	391.5	2487	360.2
70	666	448.4	1958	334.0
80	670	476.8	1561	282.2
90	655	480.1	1291	258.2
100	647	467.9	1282	254.0

$n = 10$.

The Hypothesis

We use the results of our simulation to suggest an optimal foraging strategy under this form of exploitation competition, and to propose a mechanism for passive range exclusion (the PRE hypothesis). This leads us to propose a new function for boundary marking. We then examine conditions under which exploitation rather than interference competition might be the proximate mechanism for range exclusion. The simulation made initial assumptions that we therefore include as conditions in the hypothesis, i.e. individuals cohabit in a single residence and deplete foodstuffs that, when compared to the foragers, are relatively immobile. Additional modelling would be required to determine how far these two assumptions can be relaxed, and to predict the effect of different prey depletion and renewal rates on stable range size and stable resource level in relation to harvesting.

FIG. 5. The highly significant (F = 466, $n = 50$, $P < 0.0001$) log-linear relationship between maximal gradient established within a night's foraging and group size.

PASSIVE RANGE EXCLUSION

In our simulation, food closest to the residence tended to be found first and more often than food more distant from the residence, and this pattern has been observed in the field [e.g. Johnson, 1974 (described in Johnson *et al.*, 1987); Rivault & Cloarec, 1991]. When one foraging unit from each residence was involved (equivalent to a pack or single-flock foraging species) the simulation produced largely unpredictable patterns of resource depletion. However at high forager densities the resource availability profiles in Fig. 2 were consistently obtained. This is the situation when group living species forage as subgroups or as largely independent individuals. These are "refuge" species (*sensu* Hamilton & Watt, 1970) and include for example many species of hymenoptera, bird, lagomorph, carnivore and some primates (including man). In three dimensions the resource availability profiles produced by the collective foraging activities can be envisioned as broad vortex (or inverted bell) shaped depressions of food density contours centred on the main residences [see Fig. 6(a)]. This result can also be obtained from a random diffusion model (Okubo, 1980).

The position of the ridge of high resource availability between residences will depend on the foraging pressure of neighbouring groups. This is determined by (a) the overall distribution of residence locations, (b) the relative number of foragers active from each residence, (c) the initial pattern of food distribution and its characteristics of depletion and renewal. The sigmoidal shape of the food depletion cones gives rise to a plateau of high food density, straddling the boundary isopleth of equal depletion between groups, which becomes sharper with decreasing inter-residence distances [Fig. 6(b)]. As a
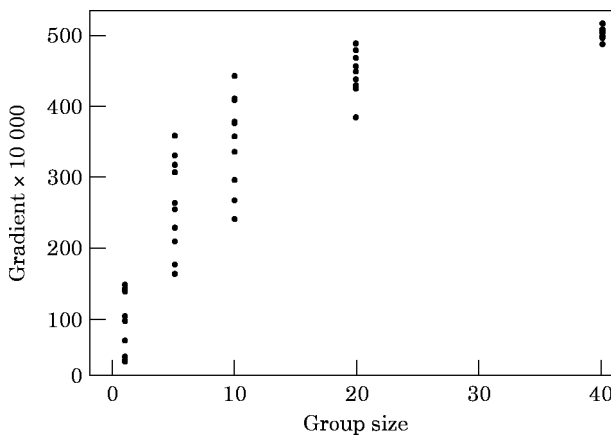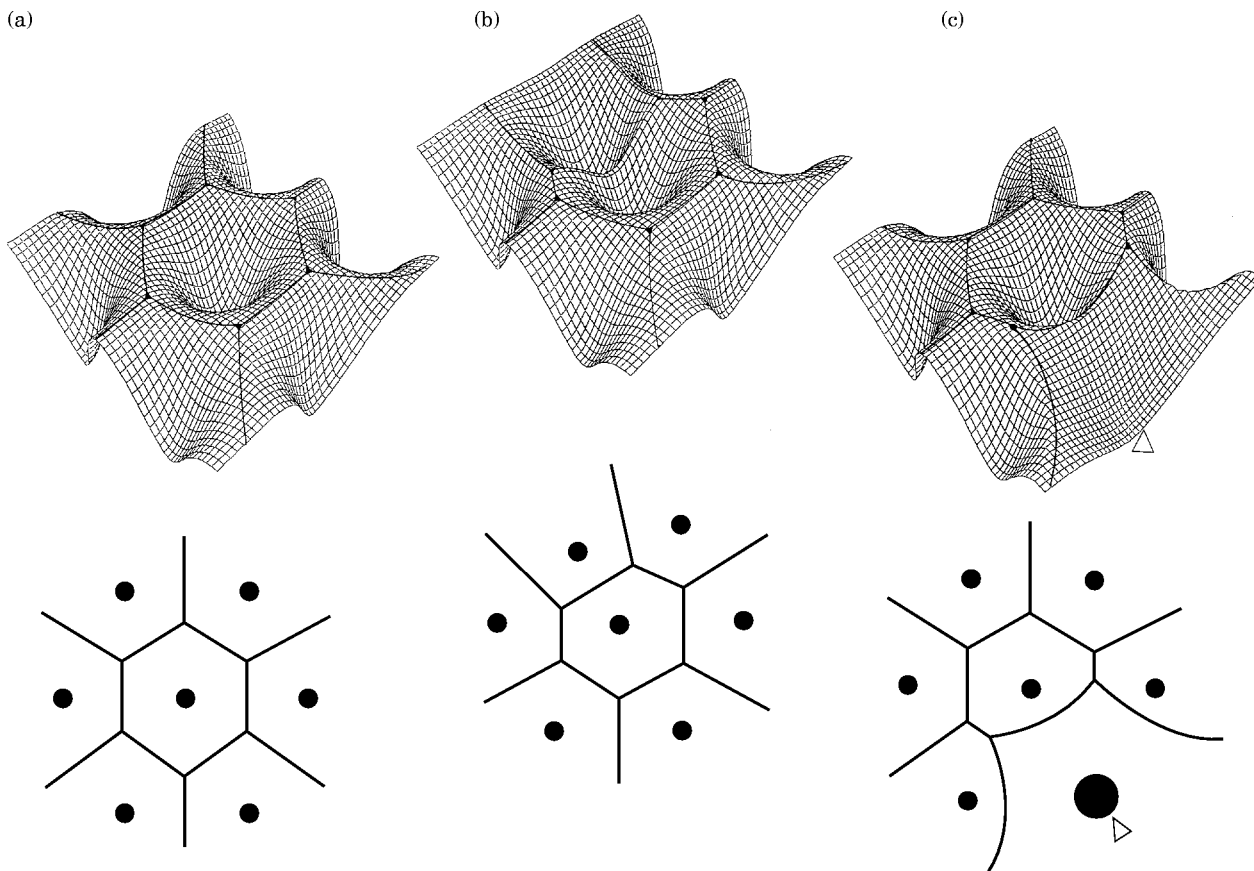
(a) (b) (c)

FIG. 6. Diagrammatic surface plots of food abundance after food density gradient establishment, with a two dimensional plot of the resulting ridge peaks, for three situations. (a) Equally sized groups that are regularly spaced; (b) equally sized groups but reduced inter-residence distance between two of the groups, note how the ridge is both lower and "sharper"; (c) regularly spaced residences with one larger group demonstrating how the larger group skews the now asymmetric ridge towards the smaller neighbouring residences. Filled circles are residence positions. Open triangle points to larger group residence in (c). See the text for details.

forager travels outwards from its main residence food availability will at first increase with distance from the main residence, then reach an asymptote at the "boundary" plateau and finally start to decrease as the forager walks towards neighbouring residences. Foragers from different residences could cross the boundary to feed on the other side of broad plateaux without significant penalty in terms of foraging success. Foragers that moved deeply into neighbouring territories or back into their own heartland too early will fare badly, as they did in our simulation. If the food gradient is later depleted and the differential equalized (see Fig. 3), the best strategy is to turn back towards the residence. In that way travelling time to return to the residence will be reduced, and hence foraging time maximized. The simulation also revealed that at lower initial food patch densities (regardless of patch richness) the gradient was not created as effectively (Fig. 4). In those conditions boundary feeding had little advantage, and players that roamed freely over the entire area scored as well as players that fed in boundary regions. In these conditions we expect range exclusion to break down.

FURTHER OPTIMIZATION OF FORAGING UNDER PRE

Our simulation corresponds to a situation in which each forager has no prior knowledge of patch location and so feeds on unexploited patches as they are encountered. Each forager acts to minimize the time it spends searching for, or travelling to, food in order to maximize the time spent feeding. Real foragers probably have partial knowledge of patch availability resulting in somewhat predictable foraging paths. Assuming the closest and richest patches are sought first this will increase the slope of the food gradient profiles and enhance the effect described here.

The decision not to continue into the neighbouring territory could be made directly on the basis of an assessment of food return with distance from the residence. If peaks in local isopleths of the food availability gradients are predictably established, foragers could remember and/or mark the location as

a guide to help optimize future foraging paths. As the gradients can alter it is likely that any boundary will still require occasional testing by deeper incursions. If the resident group can signal their foraging depletion of an area—perhaps by signalling an associated variable such as residence membership size—then incursions can be discouraged. This benefits the intruder by reducing the need for potentially suboptimal foraging during testing trips. It benefits the residents because it acts to decrease foraging pressure close to their residence (which minimizes residual depletion between foraging bouts and makes the path home more profitable). A prerequisite of the signal is that it be difficult to fake. Otherwise residents will attempt to manipulate neighbours into avoiding areas that are not depleted resulting in the intruders ceasing to heed the signal.

THE EXPRESSION OF PRE VERSUS ACTIVE TERRITORIALITY

In some species a group may be able to use active defence to monopolize a disproportionately large portion of the foraging area. In these circumstances any PRE effect will be masked. However cooperative defence of a shared territory can evolve only under certain conditions. In populations where the level of relatedness is similar between and within neighbouring groups there will be no kin selection for cooperative defence (West Eberhard, 1975). If the species forages solitarily, non cooperating individuals will be difficult to identify: it will be correspondingly unlikely that group cooperation will evolve through reciprocal altruism (Trivers, 1985), punishment (Clutton-Brock & Parker, 1995) or "common enemy" by-product mutualism (Mesterton-Gibbons & Dugatkin, 1992)—however these are potential mechanisms for the evolution of cooperative defence wherever individuals are concentrated, such as the main residence itself. That leaves group selection as a pressure for the evolution of cooperative territorial defence in refuging species (Wilson, 1990). Several authors have argued that the conditions to advance an altruistic group selected trait in the presence of intra-group competition and individual selection, are very limited [see commentaries in Wilson & Sober (1994)].

From the initial assumptions and the arguments above, we should look for strong PRE effects in species which fulfill the following criteria:

(1) Group living in a restricted location. An additional mechanism such as limited resting sites, benefit of grouping *per se* or resource dispersion is required to stop establishment of individual territories (Macdonald, 1983; Carr

& Macdonald, 1986; Woodroffe & Macdonald, 1993).
(2) Food that is not highly mobile relative to the forager and that is depleted within a foraging bout.
(3) Individuals forage solitarily or in subgroups of the whole colony.
(4) Feeding on food that has a homogenous or multi-patch distribution.
(5) Non-kin based groups, or populations with similar coefficients of relatedness between neighbouring groups.

The European Badger as a Test Case

The stochastic model was based on the spatial system of the European badger (*Meles meles* L.) in lowland England. This species largely fulfills the five criteria above. It is a group living carnivore that shares communal dens (setts). Though "outlier" setts exist, most occupation occurs at a main sett or a nearby annexe. They live in groups of typically 6 adults, with up to 26 in favourable habitats. Individuals forage largely independently of each other, feeding on food that exists as many patches around the range. The availability of their natural omnivorous diet of invertebrates and fruit is depleted by their foraging (as evidenced by their movement from patch to patch during feeding) but largely renews between foraging bouts [as evidenced by their return to those patches between consecutive nights (Kruuk, 1978a)]. Electrophoretic analysis has suggested that adult badgers in large groups have only a marginally smaller aggregate degree of kinship with their immediate neighbours than they have with members of their own group (Evans *et al.*, 1980; DaSilva *et al.*, 1994). This is due to activities such as extra-group matings, dispersal, and multi-generational breeding which tend to homogenize the degree of relatedness among contiguous social groups (Woodroffe *et al.*, 1993).

In areas with high population densities, individuals that share setts (the group) primarily defecate in specific latrine areas. These latrines may be shared by some or all members of the group (Brown *et al.*, 1992; Roper *et al.*, 1993). Such latrines may also be shared by members of the nearest neighbouring setts. As Kruuk (1978b) first showed, when plotted in plan view latrines shared between groups reveal a strikingly non-random pattern (Fig. 7). They have been termed "boundary latrines" and have been interpreted as points of boundary demarcation between contiguous territories. Discussions of badger range exclusion have tended to assume that construct

borders drawn between boundary latrines are aggressively defended by some or all members of groups against some or all members of neighbouring groups. There has been less consensus on the nature of the resources that are supposed to be defended within such a border. Candidates are non-exclusive and include food (Kruuk & Macdonald, 1985; Woodroffe & Macdonald, 1993), mates (Roper *et al*., 1986) and the sett complex itself (Doncaster & Woodroffe, 1993; Roper, 1993). While the PRE hypothesis does not preclude the possibility that any or all of these resources are actively defended, it does provide an alternative or additional role for the "border" latrines. In the PRE hypothesis the latrines shared between neighbouring groups could function as information sites that serve to signal broadly the isopleth of resource depletion between the two groups. Hence what have been interpreted as territorial boundaries, could be guides for foraging optimization between two setts. We shall stick with established convention and call the line joining the shared latrines "boundaries", but it should be understood that the PRE hypothesis does not predict that they mark the limit of a group's range. P. D.
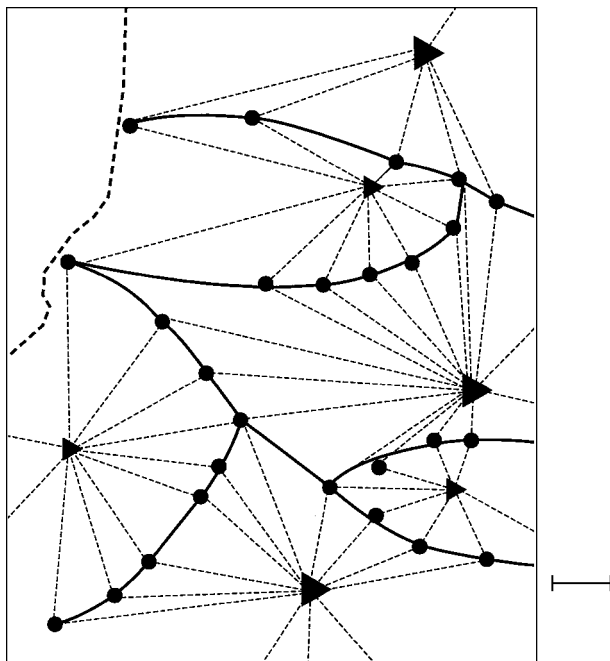

FIG. 7. Map of badger's shared latrines in a section of relatively uniform forest, Wytham, March 1993. Large triangles are sett positions for social groups of 10 adults or over, small triangles are sett positions for groups of 5 adults or under (from trap census data October 1992–November 1993). Filled circles are positions of shared latrines. The thick black line is a construct "boundary" joining latrines. Thin dashed lines are marked faeces retrievals. The thick dashed line is a fenced woodland boundary. Scale bar represents 100 m.

Stewart & D. W. Macdonald (unpublished results) propose a mechanism involving faeces matching to show how observed patterns of shared latrine use could be used to pass relatively unfakable information on the degree of resource depletion between neighbouring groups. This is not to say that the latrines cannot serve to pass additional information between groups, or that their existence may not also be exploited as a conventional border for active defence of resources including food.

We can use the predictions of PRE to distinguish its importance relative to active territorial defence (ATD) in determining the ranging patterns of badgers.

Under pure PRE a boundary area of range overlap is expected where there is amicable co-utilization of resources between groups. Core areas should remain exclusive. With pure ATD range overlap should lead to eviction or aggression when intruders are detected within a marked boundary (Richardson, 1993).

Radio-tracking has revealed extensive and consistent overlap of home ranges between members of different groups under typical conditions. This overlap does not often include core range areas around the sett (where most of a group's foraging is concentrated). As Roper *et al*. (1986) noted "the concept of a territory boundary is not an absolute one". Christian (1993) showed that the 100% group range (range encompassing all of the map grid squares where fixes were plotted) was centred around the latrine border as predicted by the PRE hypothesis, and was three times the range within the latrine boundaries. The 90% group range also extended well beyond the range of latrine boundaries, and only the core 40% range fell entirely within them. This overlap is not simply a result of badgers intruding into a territory when they are unlikely to be discovered. Though there are occasional fights (Kruuk, 1978b), members of neighbouring groups often feed side by side in boundary areas of overlap with only rare instances of aggression (P. D. Stewart & D. W. Macdonald, unpublished data; Christian, 1993). It is clearly not simply a failure in detection that allows the intrusion to continue without aggression.

Christian (1993) also observed deep territorial incursions at a farm slurry pit where invertebrates were extremely abundant. This patch was located within the latrine boundary of one group, but was used simultaneously and amicably by badgers from up to five neighbouring groups for protracted periods. Similar incursions involving fewer neighbouring groups were also found at farm grain spillages. Using the PRE hypothesis we can speculate that if a super-abundant resource is not depleted at the same

rate as the surrounding habitat it will appear as a peak in resource availability that protrudes further as the vortex of resource abundance lowers around it. Excursions into neighbouring core ranges to feed on such a resource should not be penalized in the way the PRE hypothesis predicts for resources that deplete at (or above) the average rate during the foraging period. The very rich patch should continue to be reached and exploited by groups from distances up to the threshold at which travel time to and from the patch makes feeding there relatively unprofitable. The observed high permeability of these scent-marked borders and amicable range sharing across boundaries is predicted by the PRE hypothesis but is not consistent with range exclusion by ATD.

Other predictions of PRE and ATD tend to be similar, and are borne out by observational studies. Both predict that at low food densities relative to forager densities, range overlap should increase as is observed (Neal, 1986; Roper et al., 1986; Kruuk & Parish, 1987). Similarly at very low forager density both PRE and ATD predict the observed absence or break down of range exclusion (Sleeman, 1992; Packham, 1983; Cheeseman et al., 1993).

The PRE model predicts that the boundary isopleth should be half-way between groups exerting similar foraging pressure in each other's direction (providing accessibility is the same and food patch dispersal is broadly homogenous). When one group exerts higher foraging pressure than a neighbour, it deforms the boundary isopleth so that it is closer to the smaller sett and curves towards it [see Fig. 6(c)] as has been observed (Doncaster & Woodroffe, 1993; and see Fig. 7). Doncaster & Woodroffe (1993) propose that the position of the boundaries suggest that the relative sett positions have a strong role in territory configuration. PRE provides a mechanism for this observation. ATD makes no specific predictions for boundary configuration in this case.

Discussion

Many predictions of the PRE simulation are similar to those of certain verbal permutations of ATD. As noted, the PRE hypothesis does not preclude aggressive defence of territories. It can provide an additional incentive for range exclusion when such defence is not completely effective, or it can serve as sufficient explanation in itself. In badgers the common occurrence of amicable range sharing on either side of marked boundaries is evidence for a strong role for PRE relative to ATD in maintaining core range exclusion.

The PRE hypothesis places the focus of range exclusion on the central place advantage shared by residents of the group refuge. Food monopolization is best achieved by restricting membership of this central place. Additional occupants will result in increased intra-group competition for food, which may often be more serious than between-group competition (Dunbar, 1988; Shaik Van & Noordwijk Van, 1988). We have noted that cooperative defence of a shared main residence where individuals are concentrated can evolve in species where solitary foraging precludes the evolution of cooperative range defence.

For many group living species it will be difficult to distinguish the relative influence of PRE and ATD (see for example Deslippe & Savolainen, 1995). Active defence tends to be more obvious than avoidance of an exploited area. Incomplete observations may also result in active defence of resources, such as mates, being mistaken for evidence of feeding territoriality when it occurs with PRE at foraging sites. Similarly "border" marking may, we hypothesize, arise in the context of PRE, but be misinterpreted as a conventional signal of ATD (Maher & Lott, 1995). We conclude that the role of exploitation competition as a proximate factor in maintaining range exclusion may be commonly underestimated in refuge species.

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