Shape of patch edges affects permeability.

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ABSTRACT

Emigration from one patch to another has a large effect on metapopulation dynamics. One factor that affects emigration is permeability of patch edges. This study looks at the effects of edge shape (convex, concave and straight) on edge permeability for meadow voles (*Microtus pennsylvanicus*). This was tested by mowing a strip with different edge shapes through an old field. Vole response was measured by tracking plates. Voles crossed edges at concave treatments twice as much as compared to convex and straight. Of the five different hypotheses that were considered, two were accepted: (i) edge-attraction - voles are attracted to edges, and (ii) protection - voles attempt to keep as close to the patch habitat as possible, and thus cross edges at the base of concave sections.

KEYWORDS

Dispersal, permeability, movement, metapopulations, tortuousity, meadow voles, Microtus pennsylvanicus, tracks, convex, concave

INTRODUCTION

The habitats of many animals are fragmented into patches, making emigration from one patch to another a key factor affecting population and metapopulation dynamics. And one of the key factors affecting emigration is edge permeability - the ease at which animals cross patch edges (Stamps et al. 1987). Various edge properties have been shown to affect permeability. Some edge properties are simply properties of the two adjacent habitats; for example small mammals travel further into grasslands when contrast between the two habitats is low (Lopez-Barrera et al. 2007). Some properties are actually properties of the edge itself; for example root voles (*Microtus oeconomus*) avoid approaching an edge (Lidicker 1999), and *Tribolium confusum* beetles slow down and travel more tortuously when encountering edges (Morales & Ellner 2002).

One edge property that might affect permeability, is the shape of the edge. It has long been known that tortuous edges are more permeable than straight ones, simply because there is more edge (Forman & Godron 1986). However, perhaps tortuousity of the edge itself affects permeability; perhaps animals react in some way to the shape of the edge. In a pioneering study, Hardt and Forman (1989) found that succession occurred faster in those parts of a field where it protruded into a forest, and they suggested that herbivores from the forest crossed the edges into the field more readily at concavities[1]. But since then there have been no field studies done on the reactions of animals to edge shape.

Animals might respond to edge shape in two ways. The first is a passive response, where animals do not recognize edge shape itself, but their responses to edges might create an response to edge shape as an emergent property (Nams 2010). Although animal response to edge shape has not been studied in the field, there are analogues in the response to corridors. For example, while *Eurema nicippe* and *Phoebis sennae* butterflies travel faster through habitat corridors than through habitat patches, this response is completely explained by how these butterflies reflect off of habitat edges, without there being any unique response to corridors (Haddad 1999). The second response to edge shape is an active response, where animals recognize the edge shape and in some way modify their behaviour accordingly. For example, house flies (*Musca domestica* L.) use corridors actively by specifically recognizing them and preferentially travelling through them (Fried et al. 2005).

The objective of this research was to find out how edge shape (concave, convex, straight) affects the tendency for animals to cross edges, and to test five hypotheses for the mechanism of this effect. The first three are passive ones and the last two are active; the passive ones will be tested using predictions from Nams (2010).

1) Neutral: An animal ignores the edge when it detects it, and reflects from it when it intercepts it. This predicts no difference in permeability between concavities and convexities (Nams 2010).
2) Edge-attraction: An animal tends to turn towards the edge when it detects it, and tends to travel along it for a while when it intercepts it. This has been shown by Fender’s blue butterflies (*Icaricia icarioides fenderi*) (Schultz & Crone 2001) and Eastern Bluebirds (*Sialia sialis*) (Levey et al. 2005). This predicts higher edge permeability for convexities (Nams 2010).
3) Edge-avoidance: An animal tends to turn away from the edge when it detects it and also when it intercepts it. This has been shown by Rocky Mountain parnassian butterflies (*Parnassius smintheus)* (Ross et al. 2005) and Roesel's bush-crickets (*Metrioptera roeseli*) (Berggren et

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[1] All references to concave, convex, In and Out, will be from the point of view of inside the patch. Thus a concave edge bends into the patch.

al. 2002). This predicts higher edge permeability for concavities (Nams 2010).

4) Time-minimizing: A dispersing animal attempts to minimize the time spent in inhospitable matrix, and thus travels as far as possible in the patch before crossing the edge. Thus animals would cross the edges at those parts that stick out the farthest - i.e. the convex portions. This hypothesis is exemplified by the idea that small habitat patches increase dispersal by being used as stepping stones (Fahrig & Merriam 1994). This predicts higher edge permeability for convexities and a greater effect closer to the center of the shape - thus, higher densities at the center of convexities and lower at the center of concavities.

5) Protection: An animal attempts to maximize protection while in the inhospitable matrix by keeping the patch close by. Thus animals would cross at the base of indentations into the matrix, so they could keep patch habitat on either side of them. This hypothesis was suggested by Hardt and Forman's (1989) observations of there being more herbivore-dispersed plants in fields near concave edges of forests, and it predicts higher edge permeability for concavities. This also predicts a greater effect closer to the center of the shape - thus, lower densities at the center of convexities and higher at the center of concavities.

I use meadow voles (*Microtus pennsylvanicus*) as a model animal. Small mammals are appropriate study animals because their dispersal rates fall into the range that has a great effect on metapopulation dynamics (Buechner 1989). Furthermore meadow voles are an ideal small mammal to study patch dynamics because it is easy to experimentally manipulate habitat patchiness. Meadow voles live in old fields, typically travelling in tunnels made in the dead vegetation just above level of the soil surface, and mowing creates semi-permeable barriers to voles (Collins & Barrett 1997).

METHODS

Experimental setup

I set up an experiment using mowing to make different kinds of edge shapes and then detected vole tracks in various places along the treatments. There were three edge-type treatments: convexities (called Out), concavities (called In) and straight edges. The treatments were set on both sides of a 3 m wide strip mowed through a grassy field. The strip was mowed frequently to keep grass height to a minimum. In year 2007 the treatments were paired, with individuals of the pairs ~3m apart, and pairs ~25 m apart. The pairs were considered replicates. Since this distance is greater than the average home range of a meadow vole (Harper, Bollinger & Barrett 1993), this ensured that a vole was exposed to only one treatment. In year 2008 this design was changed in order to increase sample size; treatments were single, with a spacing of 8m. This ensured that a vole was exposed to only one of each treatment type. In year 2007, 18 replicates were placed in a total length of 520m, and in 2008, 44 replicates were placed in a total length of 400m.

Vole use was sampled by tracking plates (Barrett 1983). These are 10cm square aluminium plates covered with soot. Small mammals walking over the plates leave footprints that can be identified to species group. Although it is not possible to distinguish footprints among the various vole species, the only voles present in these grassy areas were meadow voles. The plates were set at the following distances into the mowed area from the edge (**Fig. S1**): -3cm (just inside the grass), 3, 30 and 100 cm; this variable will be called distMowed. The plates were also set at the following distances to both sides of the center of the treatment, parallel to the edge: 0, 30 and 100 cm; this variable will be called distRight. For treatment In there was only one plate at distMowed = 30 and 100 because of space limitations, and for treatment Out there was no plate at distMowed = -3 and distRight = 0, because that would have ruined the tip of the treatment. Plates were replaced every 2-3 days, or whenever it rained (rain ruins the soot coating).

Numbers and directions of trails from individual animals were recorded for each plate, where one trail was defined as the record left by an animal as it crossed the plate once. If there were too many trails to count, then a coverage was estimated, from 1 to 6 (with 6 being completely covered) . Trail directions were measured such that 0° was pointing straight at the mowed area (**Fig. S1**).

Analysis

For each type of analysis I averaged the relevant statistic over the whole year for each replicate. Then each replicate was used as a sampling unit. All analyses were ANOVA, using replicate as a blocking factor.

In order to measure the overall use, I estimated trail density by the mean number of trails per plate per day. The largest number of individual trails that were distinguished was 5 per plate, and thus coverage values were assigned density values of 6-12. Trail density was normalized by a square root transformation and means were back-transformed.

I used three measures of directionality. All three were independent of each other. First was a measure of edge-following - i.e. how parallel vs. perpendicular the trails were to the edge of the mowed area. Edge-following = $|\sin(\theta_1)|-|\cos(\theta_1)|$, where θ_1 = the angle between the animal and the edge. Edge-following is -1 when the trail is perpendicular to the edge, 0 at 45°, and 1 when it is parallel to the edge.

The second measure considered directionality along the edge - i.e. how much the trail was pointed towards vs. away from the center of the treatment in a direction parallel to the edge. This will be called "To-tip". To-tip = $\sin(\theta_2)$, where θ_2 = the angle between the animal and the edge, oriented such that $\theta_2 = 0^\circ$ when pointing towards the edge. To-tip is -1 when the trail points towards the center of the treatment and 1 when it points away from the center. Thus 0 means no directionality. To-tip is undefined for the Straight treatment and for distRight = 0.

The final measure considered directionality perpendicular to the edge - i.e. how much the trail was pointed inside vs. outside of the mowed area. This will be called "To-inside". To-inside = $\cos(\theta_3)$, where θ_3 = the angle between the animal and the edge, oriented such that $\theta_3 = 90°$ when the animal points towards the inside. To-inside is 1 when the trail points towards the grass and -1 when the trail points towards the mowed area. Thus 0 means no directionality.

RESULTS

Trail density

There was a sharp drop in trail use as distance from edge increased (**Fig. 1**) - from a maximum of 1 trail every 0.73 days just inside the grass, to a minimum of about one trail every 100 days at a distance of 100cm inside the mowed area. This shows that the mowed area served as a large, but not complete, barrier to vole movement.

In order to analyse for an overall effect of treatment on edge permeability I summarized the trail densities over all values of distRight. There was an overall significant effect of distMowed, treatment, and an interaction between distMowed and treatment (**Table S1** in Supporting Information). Thus vole trail density varied among treatments, but also differently for each distMowed at each treatment. In order to track down the source of the interaction, I carried out ANOVA's for each distMowed. The only distance at which there were significant differences among treatments was at 3 cm (**Fig. 2**, **Table S2**). However, because of the low numbers of trails, the precision at distMowed = 30 and 100 was so poor that the analysis would not have even detected a doubling of use due to treatments (**Fig. 2**). Thus these distances were not included in further analyses. At distMowed=3, treatment In is significantly different (Tukey's test at p=0.05) from both Out and Straight, but there is no significant difference between Out and Straight. Thus voles enter the mowed area more often for treatment In than Out or Straight.

The final trail density analysis considered distribution along the edge (**Table S3**; **Fig. 4**a). For each treatment there were significant differences among distRight, but the differences were different for the two treatments. Specifically, voles used the plates closer to the center of the treatment for In, and further from the center for Out (**Fig. 3**). In addition, for treatment In, there was no significant effect of distMowed but there was a significant interaction between distRight and distMowed. Specifically, at distRight = 100, there were significantly fewer tracks at distMowed = 3 than -3 (F1,20 = 11.5, p = 0.003), but no significant differences at the other distRight. For treatment Out there was a significant effect of distMowed - voles used the plates more in the grassy than the mowed area (**Fig. 3**).

Directions of trails: Edge-following

Overall, voles travelled significantly more parallel to the edge than perpendicular to it (t-test, significantly different from 0, at t388=2.53, p=0.012; mean Edge-following = 0.073 ±0.0272). There was a significant three-way interaction between treatment, distRight and distMowed (**Table S4**) but no overall significant difference among treatments. Thus, I analyzed each treatment separately (**Table S5**). For treatment Out, there was a significant interaction between distMowed and distRight (**Fig. 4**b). Specifically, trails were most parallel at the center location in the mowed area, somewhat perpendicular at the next two locations in the mowed area, and parallel at the rest of the locations. For treatment In, the only significant difference was for distRight. Specifically, the plates at the center were perpendicular while the furthest ones away were parallel. For treatment Straight, there was no significant difference between distMowed, but overall, trails were significantly more parallel to the edge than perpendicular (t-test, significantly different from 0, at t_{102}=2.39, p=0.019; mean Edge-following = 0.14 ± 0.12).

Directions of trails along the edge: To-tip

Overall, voles travelled significantly more oriented towards the center of each treatment than away from it (t-test, significantly different from 0, at t118=2.80, p=0.006; mean To-tip = 0.12 ±0.08). There was a significant interaction between distRight and treatment (**Table S8**, **Fig. 4**c); specifically, for In, there was no directionality but for Out, at distRight =30 tracks were oriented towards the center, but not at distRight = 100.

Directions of trails perpendicular to the edge: To-inside

Overall, voles travelled significantly more oriented towards the mowed habitat than towards the grassy one (t-test, significantly different from 0, at t226=-4.83, p=0.001; mean To-inside = -0.14 ±0.06). The only significant differences were among distRight (**Table S8**, **Fig. 4**d); specifically, at distRight = 30 there was no significant directionality, while at distRight = 100 voles pointed towards the mowed area. There was no significant directionality at distRight = 0, but the precision was very low. There were no significant differences either among treatments or interactions with treatments.

DISCUSSION

Meadow voles more likely entered the mowed area at concavities than at convexities or straight sections. At concavities trails tended to be concentrated towards the center, while at convexities trails tended to be concentrated away from the center. Overall, trails were oriented slightly parallel to the edges, except that at concavities trails were more perpendicular closer to the center. Vole trails near the center of concavities were oriented towards the center. Overall, trails were more oriented towards the matrix than the patch habitat, especially further from the center of the edge structures.

Mechanism of effect

To test hypotheses about the mechanisms of edge shape effects, I consider what kinds of predictions they make as well as how powerful the tests are. When testing hypotheses, rejections of predictions are more powerful results than acceptances (Popper 1959) and when carrying out statistical analyses, significant differences are more powerful results than are non-significant differences (Simberloff 1990). I combined these two assessments of strengths of hypothesis

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[2] All ± are 95% confidence intervals.

tests (**Table 1**). Thus the weakest conclusion would be the acceptance of a hypothesis when no difference was predicted and no significant difference was observed, while the strongest conclusion would be rejection when a difference was predicted and a significant difference in the opposite direction was observed.

What can we conclude, given that there is not total support for one or more of the hypotheses (**Table 2**)? It is too simplistic to just count up the numbers of - vs. + in. A key factor is the exclusiveness of the hypotheses. The passive vs. active hypotheses are not mutually exclusive. However the passive hypotheses are both mutually exclusive and comprehensive - animals must react to edges in only one of these ways. On the other hand, the active hypotheses are neither mutually exclusive nor comprehensive. Animals may both try to minimize travel distance in the inhospitable matrix as well as maximize protection by staying close to the patch habitat. Or, they may do neither.

Let us first consider the passive vs. active hypotheses. Since the passive hypotheses are mutually exclusive and comprehensive, then if there is only a passive response to edge shape, then one of the passive hypotheses would be completely supported and the others would be completely rejected. The trail direction results do not show this. Thus I conclude that animals also respond actively, and that this response overrides the passive responses to edges.

Then let us consider within the active and passive groupings. The active hypotheses are neither mutually exclusive nor comprehensive. But while the hypotheses are not mutually exclusive, the experimental treatments forced a comparison between them, with each hypothesis giving the opposite predictions for convex vs. concave shapes - in effect, measuring how strong the hypotheses are relative to each other. And the results clearly show that protection is much stronger than time-minimization. Note that these treatments are not only experimentally useful, but rather, they represent the edge shapes that are relevant in nature. Edges have both convexities and concavities and we are interested in how animals respond to them. And concavities increase dispersal for meadow voles.

Among the passive hypotheses we can discount the neutral response because all of the predictions are rejected. Thus animals are either attracted to, or avoid, edges. Since the active responses override the passive ones, we can discount the density results in comparing these two. The only other result that supports edge-avoidance and not edge-attraction is a weak result, based on the acceptance of a statistically nonsignificant result (**Table 2**c). Thus we will accept the edge-attraction hypothesis.

The contradictory prediction results for the passive hypotheses may have been caused by two issues. First is that the predictions were generated under the assumption that animals did not cross the edge - edge permeability is zero (Nams 2010). Permeability of mowed edges is very low for meadow voles (Bowers et al. 1996), but it is not zero. It is not known whether a slight permeability would affect the predictions of Nams (2010). The second issue is that the predictions were generated by a specific movement model. Perhaps slightly different types of movement models would generate different predictions about edge shape effects.

In conclusion, meadow voles recognized edge shapes and respond to them when entering inhospitable matrix, by attempting to maximize protection by remaining close to the patch habitat. In addition, voles are attracted to edges in general, and although this tends to cause them to collect at convexities, this is overridden by the voles' active response of protection maximization.

Generalizations

How far into the matrix does this edge effect extend? Voles cross edges twice as readily at concavities as compared to convexities or straight edges. This is a very large effect but it is trivial if those animals do not actually traverse the matrix. Unfortunately there were too few trails at distances past 3 cm to determine how far the effect of edge shape extends. However knowing that voles actively decided to cross at concavities (the protection hypothesis), rather than simply increasing in activity there (edge-avoidance) helps in evaluating the distance. The key question is, would voles readily turn back after entering inhospitable habitat? Other studies on other dispersing animals suggest not. For example, most of the bog fritillary butterflies (*Proclossiana eunomia*) that travelled in matrix, between habitable patches, travelled with correlated random walks (Schtickzelle et al. 2007), implying that once they enter the mowed area, they do not make another decision to turn back. This implies that concavities increase movement rate at farther distances into the mowed area than just near the edge.

We can also predict vole response to edge tortuousity in general. Voles cross at concavities more often than at other edge shapes, but they cross similar amounts at convexities as compared to straight edge shapes (**Fig. 2**c). Thus voles would increase crossings at more tortuous edges, which would contain concavities, convexities and straight sections, as compared to purely straight edges. This prediction should be tested in the field.

Future studies are also needed to test my results to those seen in the wild. While my experiment was done in natural meadow vole habitats, it used manipulations that are not natural. Meadow voles typically travel in tunnels made in the dead vegetation just above the level of the soil surface; my experimental mowing cut those tunnels. Technology is making these types of studies more feasable. With the advent of GPS-based collars it is becoming easy to collect many locations of larger animals, and to relate these to habitat data collected via remote sensing (Gustine et al. 2006). This gives a new opportunity to test responses to edges for animals of other species in the wild.

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FIGURES

Fig. 1. Trail density vs. distance into the matrix from the edge of the patch (distMowed). The error bars show 95% confidence intervals. Mowed area acted as a strong barrier to vole travel.

Fig. 2. Trail density for each treatment at various distances into the matrix from the edge of the patch (distMowed). The error bars show 95% confidence intervals and the p-values refer to results of tests comparing treatments for each distMowed. The only significant difference was at 3 cm (c), where trails were about twice as dense for In as Out or Straight.

Fig. 3. Trail density at different distances along the edge (distRight) for In and Out treatments. Bars are 95% confidence intervals. The lower-case letters represent statistical comparisons within each treatment - if the letters are different, then the values are significantly different from each other. Voles made significantly more trails at the center of the In treatment than the Out treatment.

Fig. 4. Overall summary of results for each type of test. (a) Trail density: a darker shade represents a higher value of # trails/plate/day. (b) Edge-following: the flatness of the ellipse represents directionality, where a circle means no directionality and a very flat ellipse means extreme directionality either parallel or perpendicular to the edge. (c) Directionality along the edge: the length and direction of the arrows represent the directionality along the edge. Crosses represent no significant directionality. (d) Directionality perpendicular to the edge: the length and direction of the arrows represent directionality towards or away from the mowed area. Note that the directionality measures for (c) and (d) are independent of (a) and (b) - e.g. (c) measures directionality only for the component of the direction that is already along the edge.

Table 1. Strengths of hypothesis tests. "No significant difference" is deemed to be a weak test because the power of the tests is unknown.

Prediction	Observation	Conclusion	Strength of test	Symbol used in **Table 2**
difference	no significant difference	Reject	strong	-
Difference	significant difference in the same direction	Confirm	strong	+ +
Difference	significant difference in the opposite direction	Reject	very strong	- - -
no difference	no significant difference	Confirm	weak	+
no difference	significant difference	Reject	strong	- -

Table 2. Results of hypotheses tests. See **Fig. 4** for a summary of the vole trail results, **Table 1** for a description of the symbols, and Nams (2010) for direcionality predictions. A blank means that the prediction does not apply to that result.

	Hypotheses				
	Passive			Active	
Observations* about vole trails	Neutral	Edge-attraction	Edge-avoidance	Time-minimizing	Protection
Density					
Overall more trails at In than Out in mowed area		- - -	+ +	- - -	+ +
In: more trails near point than further away	- -	- - -	+ +	- - -	+ +
Out: fewer trails near point than further away	- -	- - -	+ +	- - -	+ +
Parallelism					
Parallel to edges in general	- -	+ +	+ +		
In: perpendicular at point, parallel further away	- -	- -	- -		
Out: no effect distance along edge	- -	-	-		
Directionality along the edge					
In - no directionality		-	+		
Out- towards the center		- -	- -		
Out - more directional towards the center		- -	- -		
Directionality perpendicular to edge					
In - directed towards outside	- -	+ +	- - -		
Out- directed towards outside	- -	+ +	- - -		
In - no difference closer vs further from tip		+			
Out - no difference closer vs further from tip		+			

SUPPORTING INFORMATION

The following Supporting Information is available for this article.

Table S1. Overall results of ANOVA for track density.

Table S2. ANOVA results at each distMowed for track density.

Table S3. ANOVA results for each treatment for track density.

Table S4. Overall ANOVA results for Edge-following.

Table S5. ANOVA results for each treatment for Edge-following

Table S6. Summary means for Edge-following for each treatment. A positive value means that the trails are parallel to the edge, and a negative means they are perpendicular.

Table S8. Overall ANOVA results for directionalitiy along the edge (To-tip).

Table S9. Summary means for directionalitiy along the edge (To-tip). A positive value means that the trails point towards the center of the treatment, and a negative means they point away from it. Means with different lower-case letters within the same treatment are significantly different at the p=0.05 level.

Table S10. Overall ANOVA results for directionalitiy perpendicular to edge (To-inside).

Table S11. Summary means for directionalitiy perpendicular to edge (To-inside). A positive value means that the trails points towards the inside and a negative means they point towards the outside of the patch. Means with different lower-case letters are significantly different at the p=0.05 level.

Fig. S1. Tracking plate distribution.

Table S1. Overall results of ANOVA for track density.

Source	d.f.	MS	F-statistic	P-value
distMowed	2	3.21	89.7	0.001
Treat	2	0.163	4.55	0.013
distMowed * Treat	4	0.158	4.42	0.002
Replicate	58	0.102	2.85	0.001
Error	116	0.036		

Table S2. ANOVA results at each distMowed for track density.

distMowed	Source	d.f.	MS	F-statistic	P-value
-3	Treat	2	0.301	1.87	0.16
	Error	58	0.16		
3	Treat	2	0.457	6.20	0.003
	Error	58	0.073		
30	Treat	2	0.0138	0.213	0.81
	Error	58	0.0658		
100	Treat	2	0.0079	0.237	0.79
	Error	58	0.034		

Table S3. ANOVA results for each treatment for track density.

		d.f.	MS	F-statistic	P-Value
In	distMowed	1	0.494	2.22	0.140
	distRight	2	3.39	15.2	0.001
	distMowed * distRight	2	0.823	3.69	0.028
	Replicate	20	0.514	2.30	0.0036
	Error	100	0.223		
Out	distMowed	1	6.15	56.7	0.001
	distRight	2	0.486	4.49	0.014
	distMowed * distRight	1	0.072	0.665	0.42
	Replicate	20	0.268	2.47	0.0025
	Error	80	0.108		

Table S4. Overall ANOVA results for Edge-following.

	d.f.	MS	F-Statistic	P-Value
distMowed	1	0.176	0.43	0.51
distRight	1	1.288	3.14	0.078
Treat	1	0.001	0.01	0.98
Replicate	38	0.487	1.19	0.23
distMowed * distRight	1	0.302	0.74	0.39
distMowed * Treat	1	2.758	6.73	0.01
distRight * Treat	1	0.172	0.42	0.52
distMowed * distRight * Treat	1	2.416	5.89	0.016
Error	181	0.323		

Table S5. ANOVA results for each treatment for Edge-following.

		d.f.	MS	F-Statistic	P-Value
In	distMowed	1	0.596	2.10	0.15
	distRight	2	1.293	4.56	0.012
	Replicate	18	0.213	0.75	0.75
	distMowed * distRight	2	0.228	0.80	0.45
	Error	146	0.284		
Out	distMowed	1	0.361	1.27	0.26
	distRight	1	0.878	3.09	0.082
	Replicate	20	0.569	2.00	0.014
	distMowed * distRight	2	1.935	6.81	0.002
	Error	91	0.283		
Straight	distMowed	1	0.007	0.02	0.89
	Replicate	18	0.467	1.38	0.16
	Error	83	0.338		

Table S6. Summary means for Edge-following for each treatment. A positive value means that the trails are parallel to the edge, and a negative means they are perpendicular. Means with different lower-case letters in the same treatement are significantly different at the p=0.05 level.

Treatment	Distance from center (cm)	Mean
Out	0	0.16 ±0.13
	30	0.06 ±0.17
	100	0.26 ±0.17
	overall	0.07 ±0.11
In	0	-0.15 ±0.17^{a}
	30	0.07 ±0.15^{ab}
	100	0.16 ±0.17^{b}
	overall	0.02 ±0.17
Control	overall	0.14 ±0.11

Table S7. Summary means for Edge-following for treatment Out. A positive value means that the trails are parallel to the edge, and a negative means they are perpendicular. Means with different lower-case letters are significantly different at the p=0.05 level.

distMowed	distRight	Mean directionality
-3	30	0.32±0.21^{b}
	100	0.26±0.21^{b}
3	0	0.67±0.42^{a}
	30	-0.19±0.26^{c}
	100	0.26±0.24^{b}

Table S8. Overall ANOVA results for directionalitiy along the edge (To-tip).

Effect	d.f.	MS	F-Statistic	P-value
distMowed	1	0.153	0.80	0.37
distRight	1	0.157	0.82	0.37
Treat	1	1.509	7.91	0.006
Replicate	33	0.267	1.40	0.11
distMowed * distRight	1	0.112	0.59	0.45
distMowed * Treat	1	0.015	0.08	0.78
distRight * Treat	1	1.073	5.62	0.019
Error	114	0.191		

Table S9. Summary means for directionalitiy along the edge (To-tip). A positive value means that the trails point towards the center of the treatment, and a negative means they point away from it. Means with different lower-case letters within the same treatment are significantly different at the p=0.05 level.

	Treatment	Distance from center (cm)	Mean
In	distRight	30	-0.06 ±0.08^{c}
		100	0.06 ±0.09^{c}
		Overall	0.00 ±0.06
Out	distRight	30	0.36 ±0.08^{a}
		100	0.09 ± 0.07^{b}
		Overall	0.23 ±0.05
Overall			0.12 ±0.08

Table S10. Overall ANOVA results for directionalitiy perpendicular to edge (To-inside)

Effect	d.f.	MS	F-Statistic	P-value
distMowed	1	0.000	0.01	0.97
distRight	1	0.592	4.08	0.047
Treat	1	0.004	0.03	0.87
Replicate	38	0.256	1.77	0.016
distMowed * distRight	1	0.038	0.09	0.76
distMowed * Treat	1	0.148	0.36	0.55
distRight * Treat	1	0.323	0.79	0.37
distMowed * distRight * Treat	1	0.387	0.94	0.33
Error	86	0.145		

Table S11. Summary means for directionalitiy perpendicular to edge (To-inside). A positive value means that the trails points towards the inside and a negative means they point towards the outside of the patch. Means with different lower-case letters are significantly different at the p=0.05 level.

Treatment	Distance from center (cm)	Mean
distRight	0	-0.18 ±0.77^{ab}
	30	-0.096 ±0.10^{b}
	100	-0.24 ±0.11^{a}
Overall		-0.14 ±0.06

Fig. S1. Tracking plate distribution.

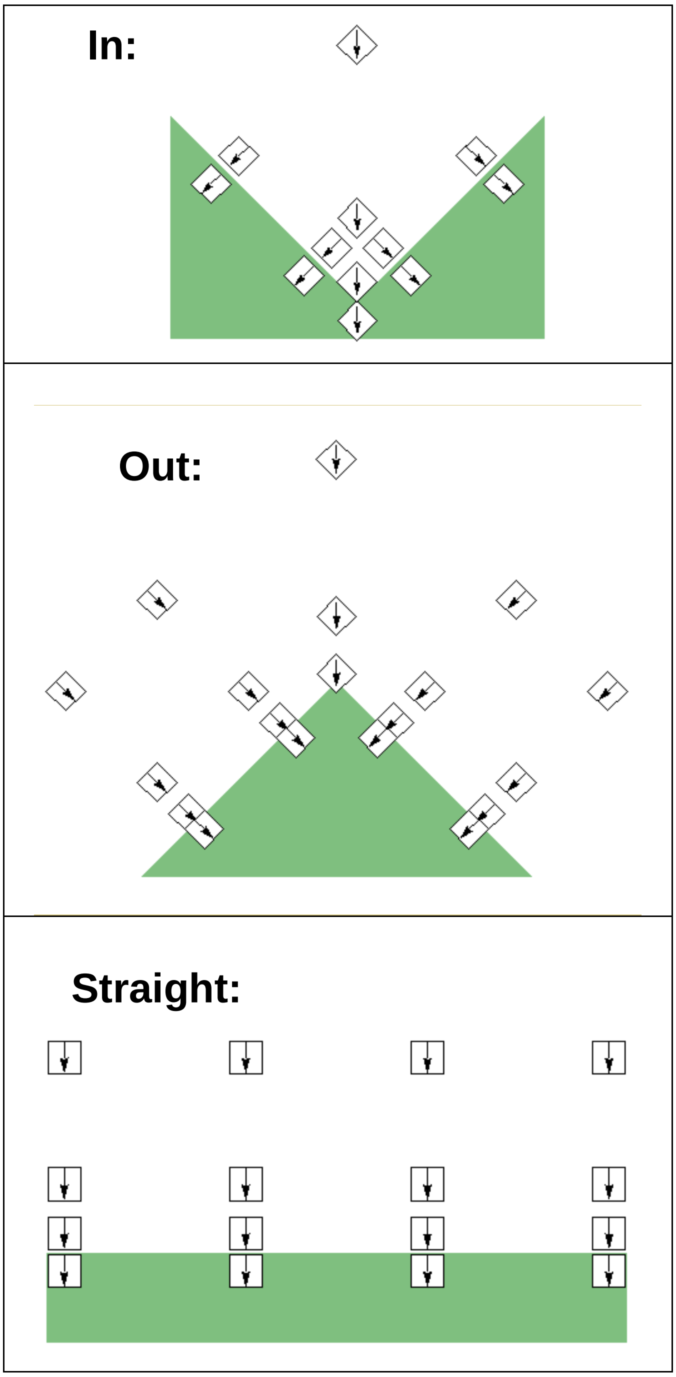
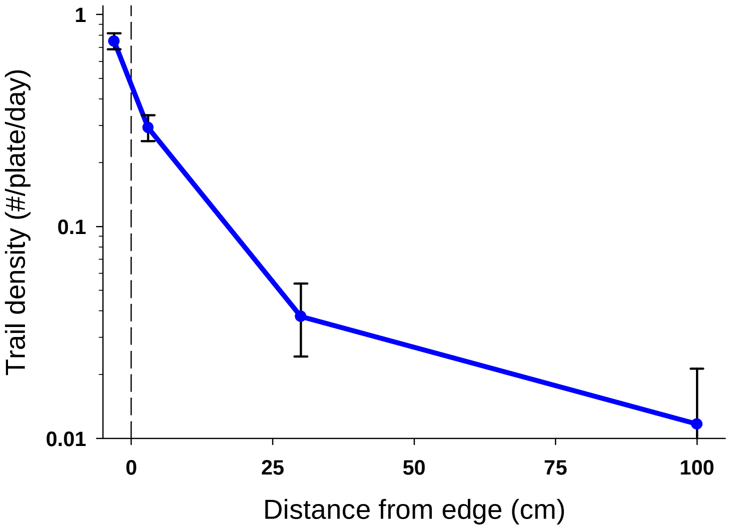
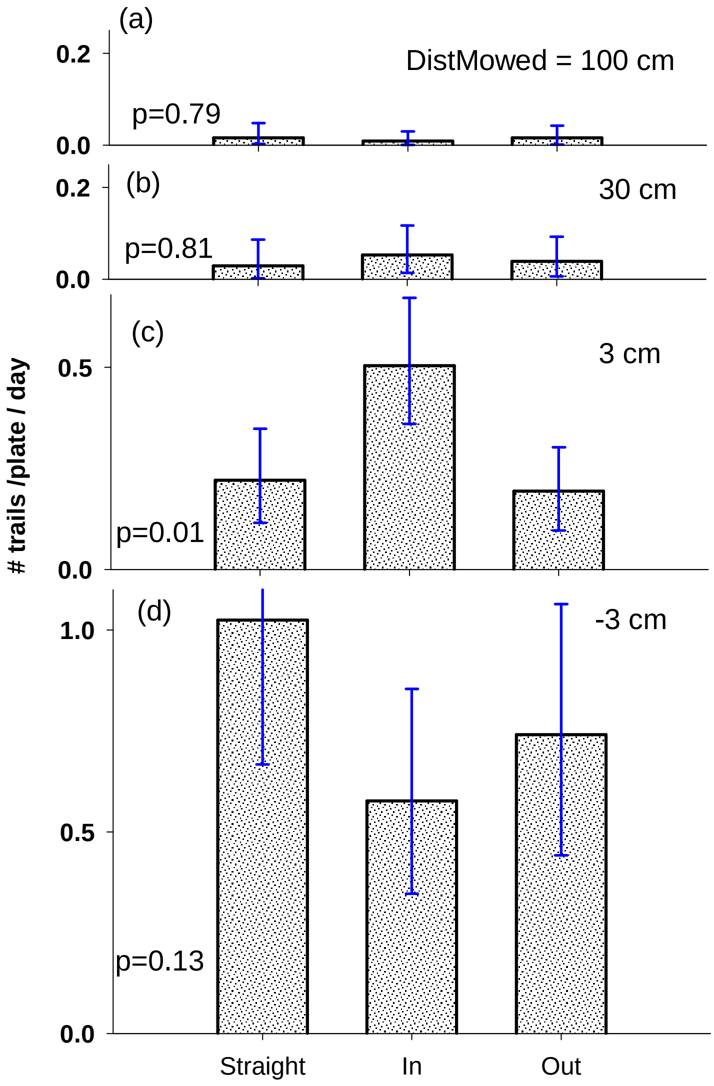


Fig. 1



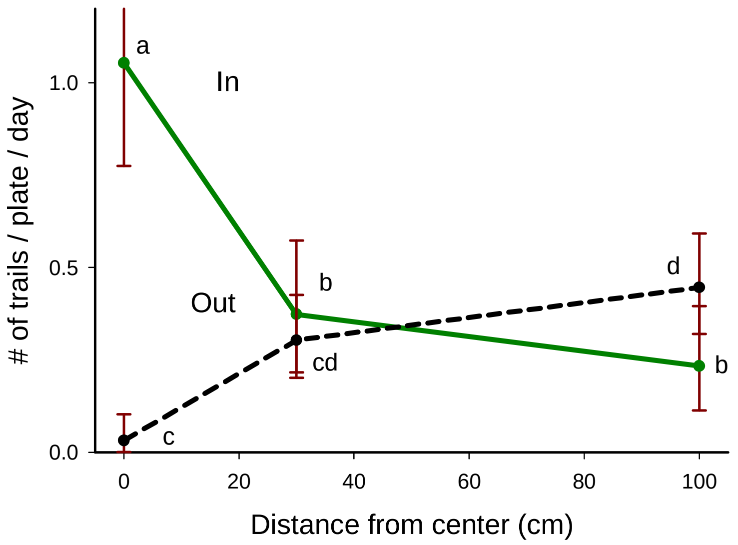
1
0.1
0.01
Trail density (#/plate/day)
0
25
50
75
100
Distance from edge (cm)

Fig. 2



(a)
DistMowed = 100 cm
p=0.79
0.2
0.0
(b)
30 cm
p=0.81
0.2
0.0
(c)
3 cm
p=0.01
0.5
0.0
(d)
-3 cm
p=0.13
1.0
0.5
0.0
trails /plate / day
Straight
In
Out

Fig. 3

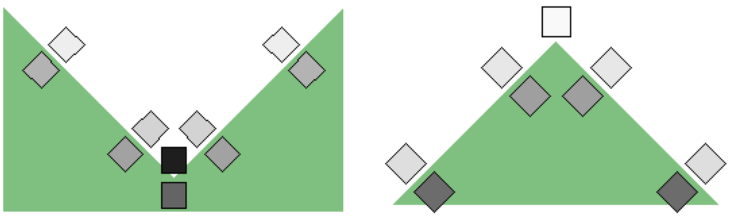


a
In
1.0
0.5
0.0
# of trails / plate / day
b
Out
d
cd
b
c
0
20
40
60
80
100
Distance from center (cm)

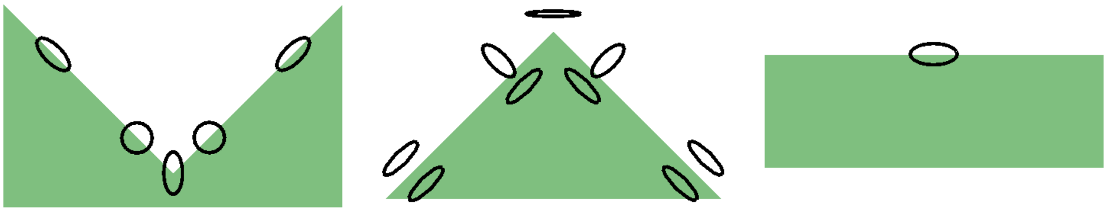
Fig. 4

In Out Straight

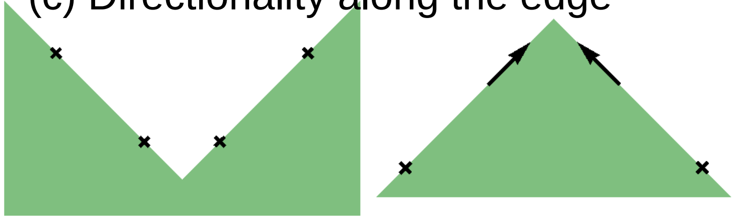
(a) Trail density



(b) Direction: parallel vs perpendicular



(c) Directionality along the edge



(d) Directionality perpendicular to the edge