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Can foraging behaviour reveal the eco-evolutionary dynamics of habitat selection?

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ABSTRACT

Rationale: Adaptive behaviours, particularly those related to resource harvest and the time available for fitness-enhancing activities, may serve as suitable surrogates for fitness.

Methods: I explore this potential link between behaviour and eco-evolutionary dynamics with controlled field experiments. The experiments manipulated densities of meadow voles foraging in large replicated enclosures. I used the lock-step connection between resource harvest and fitness to generate three fitness surrogates: giving-up densities from artificial resource patches, quitting-harvest rates, and time available for non-foraging behaviours that enhance fitness.

Results: Per capita consumption from food trays did not change with population size. Time allocated to foraging increased with population density. Quitting-harvest rates in both safe and risky patches declined linearly with population density. The total amount of time necessary for a new individual to acquire sufficient energy for maintenance increased hyperbolically. Invasion landscapes based on the three fitness surrogates yielded the same behaviourally and evolutionarily stable strategy (ESS) of habitat selection. But the fitness benefits, subsequent convergence towards the ESS, and potential variation about the ESS, varied.

Conclusions: Adaptive foraging behaviour is a reliable and rapid metric for assessing the evolutionary stability of habitat selection. This proof of concept suggests that behavioural metrics may play a prominent role in assessments of other strategies. We may even be able to use behavioural metrics to forecast ecological and evolutionary futures associated with ecological change.

Keywords: adaptive landscape, evolutionarily stable strategy, fitness, foraging behaviour, habitat selection, harvest rate, meadow vole, patch residence time.

INTRODUCTION

Solutions to density- and frequency-dependent evolutionary games, such as habitat selection, require assessments of the fitness of alternative strategies near their respective ecological equilibria (e.g. Doebeli, 2012). The solutions can easily be visualized by imagining a fitness landscape oriented along a cline of strategy values [but see an astute cautionary commentary by Pigliucci (2012)]. It follows that a convenient definition of adaptive evolution

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is a change in the topography of the fitness landscapes of relevant strategies. Evolutionarily stable strategies (ESS) rest on a peak or ridge of high fitness, or lie (perhaps momentarily) in a valley or other depression of low fitness, in those landscapes (e.g. Vincent and Brown, 2005; Morris and Lundberg, 2011; Hendry *et al.*, 2012, and many others). The fitness landscape is thus both a metaphor (Svensson and Calsbeek, 2012) and model (Hendry and Gonzalez, 2008) for adaptive evolution.

Although implicit analysis of the dynamics of fitness landscapes is essential if one is to calculate the ESS, their use as an empirical tool is limited by difficulties in assessing the density-dependent fitness of competing strategies. These difficulties include the constraints of manipulating or controlling density without altering underlying strategies. Empirical ecologists face a host of additional problems associated with defining and measuring fitness (e.g. Hunt and Hodgson, 2010).

I aim to evaluate whether the task of assessing fitness landscapes can be simplified by using behavioural surrogates in place of fitness. Such surrogates must share four properties: (1) candidate behaviours must be tightly linked to key fitness components of reproduction, survival, and dispersal; (2) the behaviours must vary with density and the frequency of alternative strategies; (3) behaviours dedicated to one task must be traded off against others; and (4) the behaviours must be readily quantified in the field. Foraging behaviour meets each of these criteria. Foraging provides the energy for reproduction and varies with density and energetic state. Time spent on apprehension and vigilance reduces foraging efficiency (e.g. Lima and Dill, 1990; Dall *et al.*, 2001; Brown and Kotler, 2004). Foraging behaviours are linked closely to patch use and habitat selection (Rosenzweig, 1981; Morris and Davidson, 2000), and can often be inferred from relatively simple experiments measuring either foraging time or the amount of resource remaining in artificial resource patches [giving-up density (e.g. Brown, 1988; Brown and Kotler, 2004)].

Thus, I describe an experiment that manipulated the density of meadow voles in paired enclosures while I measured their giving-up densities (GUDs), and time spent foraging, in depleting food patches. I combine GUDs and foraging time to calculate quitting-harvest rates (QHRs). I use those rates to estimate the amount of time voles living at different population sizes require to meet their non-reproductive (survival) energetic requirements. The residual time available (RTA) represents the 'surplus' that can be allocated towards fitness-enhancing activities such as resting, mating, and acquiring energy to support gestation and lactation. I then use the density-dependent GUDs, QHRs, and RTA to calculate the fitness advantage obtainable by voles that play an unbeatable strategy of habitat selection compared with others that play any other strategy of habitat use. I compare the invasion landscapes generated from each fitness surrogate. The varying topographies of the landscapes specify the same ESS of habitat selection, but with dramatically different fitness trajectories and expectations for residual density variation about the ESS. The experiment's novel insights promise an exciting future for those who would dare to use one or more adaptive behaviours to reveal the evolutionary stability of other strategies.

Fitness invasion landscapes for habitat selection

Imagine a population where individuals have a choice to occupy one of two equal-sized and identical patches of a single habitat within which populations grow logistically:

$$\frac{dN}{dt} = rN\left(1 - \frac{N}{K}\right)$$

where N is population density, r is the population's maximum instantaneous growth rate, and K is its carrying capacity. Dividing both sides by N yields the per capita population growth rate:

$$\frac{1}{N}\frac{dN}{dt} = r - \frac{rN}{K}$$

(linear density dependence). Assume that individuals are coarse-grained (Levins, 1962, 1968) and can occupy either patch without cost. The population will achieve the strategy of an ideal free distribution (Fretwell and Lucas, 1969) whenever the population density and its associated per capita growth rate are equal in the two patches. However, many different combinations of density in the two patches are possible at any given total population size ($N_1 + N_2 = N_{total}$). Regardless, our estimate of fitness (i.e. per capita population growth) from each possible density is generated from a single growth-rate function. Thus, the expected fitness of an additional individual for any strategy (defined as the proportion of individuals in one of the patches) is the weighted geometric mean fitness obtained from the two patches (Levins, 1962, 1968):

$$\bar{W} = \left\{\left[r - \frac{r(N_1+1)}{K}\right]^{p}\right\}\left\{\left[r - \frac{r(N_2+1)}{K}\right]^{(1-p)}\right\}$$

where p and $1-p$ represent the proportion of the population living in patches 1 and 2 respectively.

The strategy that maximizes the weighted per capita growth rate can be calculated from the neighbour invader strategy (NIS) landscape, a graph of the fitness of an individual playing one strategy assuming that all other individuals 'in the neighbourhood' are playing either that strategy or some other (Apaloo *et al.*, 2009). The evolutionarily stable density- and frequency-dependent strategy is revealed along the valley bottom of the NIS landscape where the stable strategy cannot improve on its own fitness (Apaloo *et al.*, 2009). The valley floor thus corresponds with the habitat isodar (Morris, 1988, 2011), the set of densities such that an individual's expected fitness is identical in the two habitats. The valley walls represent the density- and frequency-dependent fitness advantages of the strategy relative to others.

Our example contains only two patches of one habitat. We can calculate an individual's fitness for every possible proportion of individuals occupying them. To draw the landscape, we imagine an individual that always occupies the single patch-type maximizing its fitness. We then graph the density-dependent fitness of such an individual for all scenarios in which the rest of the population plays all possible strategies. Given our assumptions of a linear fitness function in replicates of a single habitat, the V-shaped global fitness invasion landscape is perfectly symmetrical about the $p = 0.5$ strategy (Fig. 1).

Although it is easy to conceptualize and graph a hypothetical fitness-invasion landscape as in Fig. 1, doing so in practice is complicated by two major logistical and practical difficulties. First, we must define and estimate fitness in different habitats. Second, we must simultaneously estimate density in order to infer the density- and habitat-dependent shapes of the fitness functions. So it would be wise to search for simpler, and possibly more reliable, correlates of fitness.

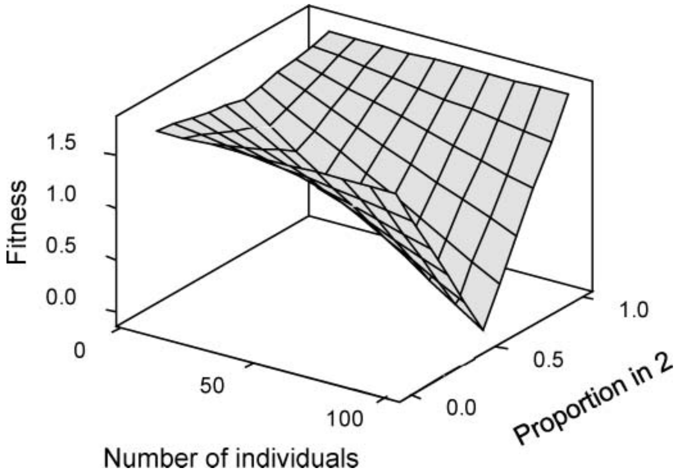

Fig. 1. An illustration of the global fitness invasion landscape generated for two identical and equal-sized habitat patches assuming cost-free dispersal and logistic population growth. The unbeatable strategy (equal density in both patches) occurs along the symmetrical valley floor. Parameter values: $r = 1.8$, $K = 50$.

Foraging behaviour as a surrogate for fitness

Fitness entails procuring resources for growth, maintenance, survival, and reproduction. It follows that any behaviour that allows one to calculate resource procurement can be used as a surrogate for fitness. The most obvious candidates are those emerging from the behaviour of foraging individuals. Suitable metrics might include giving-up densities (GUDs) or times, quitting-harvest rates (QHRs), and the time available to acquire resources beyond those required for growth and maintenance.

Foraging metrics rely on the key prediction from the marginal value theorem (Charnov, 1976): an individual feeding in depletable patches within a habitat should cease foraging (GUD) when the rate of resource harvest from any given patch is equal to the mean rate from all exploited patches in the habitat. That rate is the QHR (and the GUD is the resource density associated with it). Foraging metrics will be further modified by a variety of costs (Bedoya-Perez *et al.*, 2013), including those associated with energy expenditure while foraging, predation risk in the patch, and missed fitness opportunities elsewhere (Brown, 1988). The GUD and QHR will decline with the density of foragers as they deplete resources in all patches. Thus, if energy is correlated with fitness, density-dependent GUDs and QHRs should be reliable surrogates for fitness, particularly when we collect GUDs and QHRs from a single habitat in which there is one density-dependent fitness function.

Giving-up densities and quitting-harvest rates no doubt provide a measure of patch and habitat quality. But it is unclear how, and how well, individuals integrate density-dependent fitness costs into their foraging decisions. Thus an alternative approach might be to calculate the expected residual time available for additional foraging and other activities to support reproduction after an individual procures enough resources to maintain its non-reproductive state. This time can be estimated from density-dependent QHRs if one also knows: the individual activity period (= maximum time available for foraging); the energetic value of the resource; the organism's digestive efficiency; and the metabolic demands for growth and maintenance.

METHODS

I conducted experiments in four adjacent 50 × 50 m vole-proof enclosures in an old-field-young-pine plantation in northern Ontario, Canada (full details of all methods, as well as their limitations, are described in the appendix: evolutionary-ecology.com/data/2884Appendix.pdf). I placed four pairs of plastic resource trays in each of the quadrants of each enclosure. Each tray contained 8.0 g of whole oats mixed thoroughly into 1.5 litres of sieved silica sand. I paired adjacent enclosures (E1 with E2; E3 with E4) to create, as best as possible, two sets of identical 'habitats'. I designed the experiment so that I could monitor meadow-vole foraging at different controlled population sizes.

My assistants and I removed all 'resident' voles from the enclosures during an intense three-day trapping period spanning 10–12 July 2012. We then added 21 male and 21 female voles to each pair of enclosures (84 voles in total) using voles trapped nearby. I implanted radio-frequency identification (RFID) tags into these voles and allocated equal sex ratios (21:21) of voles to the two pairs of treatment enclosures.

We habituated the voles to the 32 foraging trays (eight in each enclosure), before live-trapping the voles at four-day intervals. We moved equal numbers of randomly chosen males and females from one enclosure of a pair to the other during each trapping interval. The design yielded 16 different possible densities in each pair of enclosures.

We allowed voles at each specified density to forage in the trays for three consecutive days. We collected the trays each day and replaced them with a duplicate set while we cleaned and weighed the uneaten oats. Voles had access to all trays for 23 hours. We did not observe voles directly, but monitored their individual and cumulative foraging times (0.01 second accuracy) with the RFID antennae placed under two pairs of trays in each enclosure (16 in total). We removed trays on the fourth day and downloaded the foraging time data.

We completed the experiment with three consecutive days of live-trapping. I used the final trapping data, the records of vole captures throughout the experiment, and the RFID data to calculate the minimum numbers of voles alive during each 4-day interval.

Giving-up densities and quitting-harvest rates

I calculated mean GUDs separately for open and covered trays across all four stations in each enclosure for each of the density comparisons. I then calculated the amount of oats consumed (8.0 g – GUD) from individual trays, and tabulated the total time that voles foraged in trays. Mean GUDs were unexpectedly high in enclosure E2 during the first foraging interval. I attributed this departure to voles being insufficiently familiar with the experimental arena, so I deleted data collected during the first interval. I also deleted cases involving time when our equipment malfunctioned (as when thunderstorms caused power interruptions), three cases when voles may have burrowed under trays, and data at very low density with no foraging. I used the remaining data to plot the harvest curve (consumption in grams versus time spent foraging) in each type of tray.

I used Akaikie's Information Criterion [AIC (Burnham and Anderson, 2002)] to select the best model describing the harvest curve (full details in 2884Appendix.pdf, *Giving-up densities and quitting-harvest rates*). I used the derivative from that curve to calculate the instantaneous QHR. Next, I generated a predictive equation for the effect of density on mean QHR and evaluated whether the relationship was homogeneous between covered and open trays (ANCOVA; dependent variable = mean QHR, independent variable = type of tray, covariate = minimum number of voles known alive). The ANCOVA revealed that density-dependent QHRs differed between open and covered trays, so I generated separate prediction equations for each type of tray (linear regression; dependent variable = mean QHR, independent variable = minimum number of voles known alive). I did the same for the mean GUD.

Energy requirements and residual time available

I calculated energy requirements for maintenance by an adult meadow vole from equation 2 in Innes and Millar's (1981, p. 786) assessment of energetic costs for female voles:

$$\textit{daily energy for maintenance} = (5.57 \times 0.89) \times 17.8 = 88.3\ \text{kJ} \cdot \text{day}^{-1}.$$

I used the estimate of 88.3 kJ, and the energy content of whole oats (2884Appendix.pdf, *Energy requirements*) to calculate the daily consumption of oats (7.07 g) required for maintenance.

I solved the relationship between the mean mass of oats eaten in a tray and population density with linear regression through the origin. I multiplied this value times the number of trays. The product yields the amount of the voles' expected energy for maintenance that was obtained from oats. I assumed that the proportion of time allocated to foraging in trays over the 23-hour foraging period [meadow voles are active both day and night (Madison, 1985)] corresponded with the proportion of energy consumed from trays. I subtracted the predicted foraging time from the total time available to forage in the trays. The difference is the estimated maximum residual time available (RTA) to a vole foraging only in trays at the density-dependent QHR. The RTA corresponds to the amount of time potentially available to acquire energy beyond that needed for maintenance.

Fitness invasion landscapes

I drew a total of six invasion landscapes. Each landscape assessed the value of the fitness surrogate that a newly arriving individual would attain if it played the unbeatable 'move to maximize fitness' strategy while all other individuals played that strategy, or a different one. I drew four of these landscapes directly from GUDs and QHRs separately for open and covered trays. I drew a fifth landscape using RTA. I also calculated residual time available following foraging to draw a sixth landscape but assumed that all voles, including the newly arrived one, obtained an equal share of the habitat's resources (rather than the reduced share obtained only from trays when the new vole starts to forage at the QHR).

Statistical analyses were conducted in SPSS (version 21), MINITAB 13, and R (R Development Core Team, 2008). All methods conformed to the guidelines of the Canadian Council of Animal Care as approved by Lakehead University's Animal Care Committee.

RESULTS

Density treatments

Population densities in both treatment pairs declined during the study (Table 1). I attribute the decline to natural predators as well as to a feral cat. The cat's nocturnal presence was recorded in images from motion-activated wildlife cameras adjacent to the enclosures. Nevertheless, my assistants and I were able, in all intervals except the final one, to move the targeted number of voles from one enclosure to the other (Table 1). Although densities declined through time, differences in realized density (minimum number of voles known alive) among enclosures were qualitatively similar to the targeted values (Table 1; 2884Appendix.pdf, *Field protocol*). There was thus a sufficient range of densities to assess density-dependent differences in foraging behaviour.

Giving-up densities

Giving-up densities were consistently lower in covered trays than in the open trays (mean GUD under cover = 2.59 g, mean GUD in open = 5.53 g; paired $t = -30.2$, d.f. = 383, $P < 0.001$). There was a marginal difference in GUDs between open and covered trays among enclosures ($F_{3,380} = 2.47$, $P = 0.061$). This model accounted for less than 2% of the variance in the data, so I pooled the data for subsequent analyses.

Harvest curves

Voles foraged differently in enclosure E1 than they did in the other three enclosures (2884Appendix.pdf, *Fig. A1*). I attributed this effect to the lower tree density in that enclosure (2884Appendix.pdf, *Field protocol*), and deleted the enclosure E1 foraging data.

Table 1. A comparison of target and realized densities of adult meadow voles used in experiments designed to evaluate the eco-evolutionary dynamics of density-dependent habitat selection in Lakehead University's Habitron in northern Ontario, Canada

	Treatment 1				Treatment 2			
	Target density		Realized density		Target density		Realized density	
Interval	E1	E2	E1	E2	E3	E4	E3	E4
1	8	34	8	29	8	34	6	26
2	24	18	24	13	24	18	22	8
3	12	30	11	24	12	30	8	22
4	28	14	27	8	28	14	24	6
5	16	26	15	20	16	26	11	18
6	32	10	30	4	32	10	27	2
7	20	22	15	16	20	22	10	14
8	36	6	24	6	36	6	14	7

Note: Density = minimum number known alive. Target densities refer to those expected after moving equal sex-ratios of voles from one treatment enclosure to the other. Targeted numbers for movement were attained in all intervals except '8' when four voles were moved from E4 to E3 and seven voles were moved from E2 to E1. E1–E4 correspond to the four field enclosures.

I used the remaining data to assess three potential explanatory models (linear, quadratic, and exponential; Table 2). Of the three, the quadratic expression [oats eaten = 4.753*hours foraging – 0.708*(hours foraging)^2, $P < 0.001$ for both coefficients] yielded the largest R^2 (the exponential model had the lowest) and a much lower AIC than the linear model (Table 2, Fig. 2).

Quitting-harvest rates

The means of the voles' instantaneous quitting-harvest rates ($g \cdot h^{-1}$) [derivative of the quadratic-regression equation, QHR = 4.753 – 2(0.708)*(hours foraging); negative asymptotic values converted to zero; zero transforms explained in 2884Appendix.pdf, *Giving-up densities and quitting-harvest rates*] declined linearly with increasing population

Table 2. Harvest curves for meadow voles foraging in covered and open trays in the Lakehead University Habitron in northern Ontario, Canada

Model	*F*	d.f.	*P*	R^2	AIC	ΔAIC
Time (linear)	951.8	1,154	<0.001	0.86	618.6	130.1
Time + Time^2 (quadratic)	**1211.8**	**2,153**	**<0.001**	**0.94**	**488.5**	**0**
Log$_{10}$Time (exponential)	763.1	1,154	<0.001	0.83		

Note: The selected model is indicated in **bold** type. All models assessed by linear regression forced through the origin; dependent variable = mass of oats eaten (models with time and time^2); mass of oats eaten was log-transformed for the exponential model ($y = bx^a$). Time = hours in foraging tray, AIC = Akaikie's Information Criterion, ΔAIC = difference from the model with the smallest AIC (AIC not calculated for the exponential model because it used a different dependent variable).

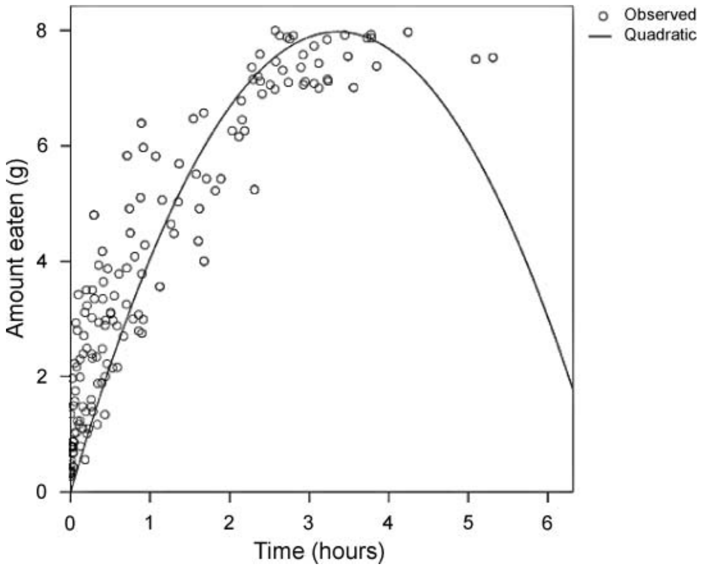

Fig. 2. The harvest curve generated from a quadratic regression of meadow voles foraging for oats in open and covered trays at the Lakehead University Habitron in northern Ontario, Canada.

density (Fig. 3). The decline differed between open and covered trays (tray × density interaction, $F_{1,10} = 21.88$, $P = 0.001$, repeated-measures ANCOVA; mean QHR in open = 4.769 – 0.026 density, $F_{1,10} = 4.78$, $P = 0.054$; mean QHR in cover = 4.029 – 0.146 density, $F_{1,10} = 25.97$, $P < 0.001$; Table 3).

Voles foraged much longer under cover (mean = 2.2 h, s.d. = 0.92) than in the open (mean = 0.27 h, s.d. = 0.22). Voles allocated an average of 0.12 h foraging in the open for

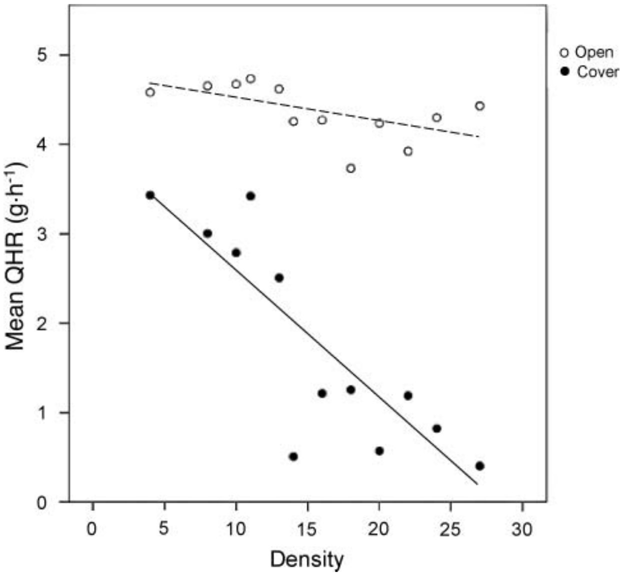

Fig. 3. Relationships between mean quitting-harvest rate (QHR) and density of meadow voles feeding in covered (solid line) and open (dashed line) foraging trays in the Lakehead University Habitron in northern Ontario, Canada. Lines fitted by overlaying actual relationships onto the scatterplot.

Table 3. Linear regression statistics for comparisons between mean quitting-harvest rate and density and between mean time foraging and density

Tray	Comparison	*F*	*t*	d.f.	*P*
Mean QHR					
Open	Model	4.775		1,10	0.054
	Intercept		23.93	10	<0.001
	Slope		–2.185	10	0.054
Cover	Model	25.97		1,10	<0.001
	Intercept		8.336	10	<0.001
	Slope		–5.096	10	<0.001
Mean time foraging					
Open	Model	32.36		1,11	<0.001
	Slope		5.689	11	<0.001
Cover	Model	285.645		1,11	<0.001
	Slope		16.901	11	<0.001

every hour that they foraged under cover. The mean amount of time that voles engaged in foraging increased with density, but at different rates in the open than under cover (tray × density interaction, $F_{1,10} = 27.41$, $P < 0.001$, repeated-measures ANCOVA; mean hours in open = 0.018 density, $F_{1,11} = 32.36$, $P < 0.001$; mean hours under cover = 0.138 density, $F_{1,11} = 285.64$, $P < 0.001$; both regressions forced through the origin; Table 3, Fig. 4).

Calculations for time available after foraging

Mean oat consumption in a tray increased linearly with population density [consumption (g) = $0.244 \cdot N^{-1}$, $F_{1,13} = 145.008$, $P < 0.001$, $R^2_{\mathrm{adj}} = 0.91$ (Fig. 5)]. This value corresponds to 1.95 g oats per vole (0.244 × 8 trays in each of the three enclosures used for the calculation, = 27.61% of the daily energy requirement for maintenance). I assumed that the amount of time voles foraged outside of the trays was the same fraction as that represented by the proportion of food required for maintenance (1 – 0.2761 × 23 h = 16.65 h). I used the assumption and the per capita resource requirement to calculate the time available for activities other than foraging by a new vole entering the population at the QHR [RTA, the maximum time available to forage in trays (6.35 h) minus the density-dependent amount of time required for voles to consume 1.95 g of oats from the trays]. This RTA would be appropriate for those cases when residents restrict newly arriving voles to sub-optimal patches.

The amount of foraging time needed to meet maintenance requirements increased hyperbolically with density (Fig. 6). This pattern reflects the rapid decline in harvest rates associated with the diminishing foraging returns in the trays (Fig. 2). A vole entering a

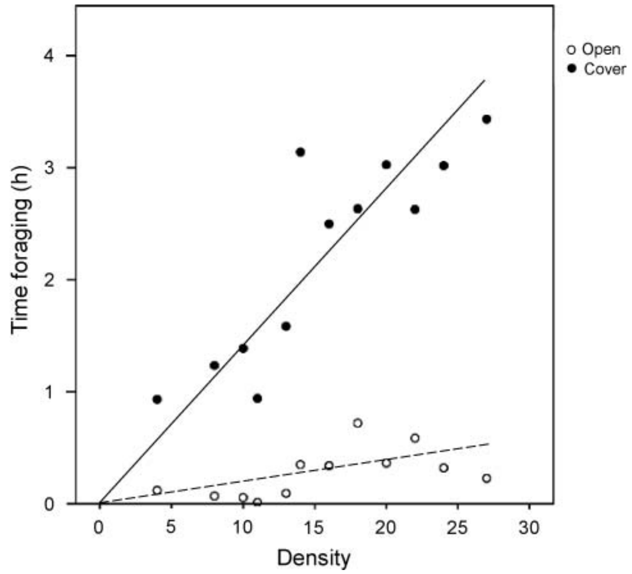

Fig. 4. Relationships between time spent foraging in covered (solid line) and open (dashed line) trays in the Lakehead University Habitron, northern Ontario, Canada. Lines fitted by overlaying actual relationships onto the scatterplot.

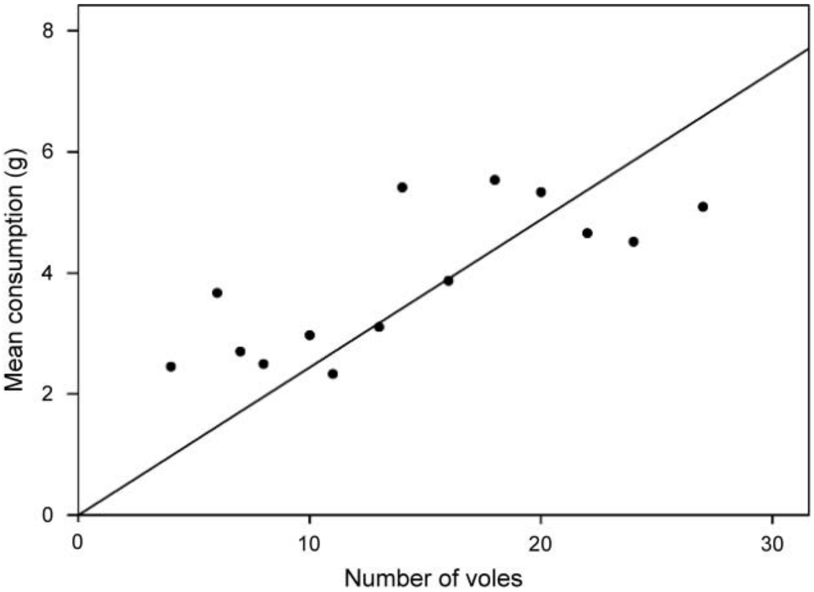

Fig. 5. Relationship between the mean amount of oats consumed from a foraging tray and the number of voles living in an enclosure at the Lakehead University Habitron. Note that the different scales for the two axes distort the tight fit with a linear model.

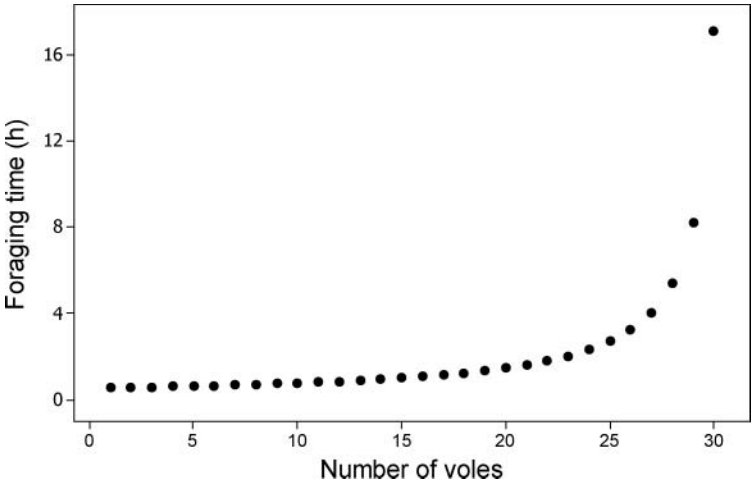

Fig. 6. The foraging time needed to meet the energetic requirements of adult meadow voles feeding in covered and open foraging trays in the Lakehead University Habitron, northern Ontario, Canada.

population with 28 or more individuals, and foraging at the density-dependent QHR, would be unable to acquire sufficient energy for maintenance (foraging time in trays by 28 voles = 5.05 h; by 29 voles = 7.67 h; maximum available = 6.35 h).

The RTA calculated for a new vole entering the population at the existing QHR is likely too stringent. An optimal forager's QHR occurs when foraging benefits equal foraging costs (Brown, 1988). Voles should thus be expected to attain a positive energy balance while foraging. Given that per capita oat consumption was constant (Fig. 5), it is reasonable to assume that all foraging individuals obtained an equal share of the harvest. I generated a second model to account for this likelihood. I calculated the time required for a new vole, entering a population with different numbers of residents, to attain the population's density-dependent QHR. I assumed, as above, that voles allocated 27.61% of their foraging time to trays and used this value to calculate the expected density-dependent time that individuals foraged elsewhere in the habitat. I calculated the time available for non-foraging activities as 23 h minus the sum of these two time estimates (caveats associated with these calculations are addressed in 2884Appendix.pdf, *Caveats*).

Invasion landscapes associated with GUD and QHR

Invasion landscapes for GUDs and QHR were virtually identical because the two variables were linearly redundant with one another (mean GUD under cover = 1.4 mean QHR under cover − 0.36; $F_{1,10} = 488.0$, $P < 0.001$, $R^2_{\text{adj}} = 0.98$; mean GUD in open = 0.84 mean QHR in open − 1.9; $F_{1,10} = 165.2$, $P < 0.001$, $R^2_{\text{adj}} = 0.94$). Thus, I illustrate only the landscapes generated for GUDs (Fig. 7) (the landscape for QHR is displayed in 2884Appendix.pdf, *Fig. A2*). Each landscape sinks with density and changes shape (the valley is deeper at high than at low density), and reveals a single stable strategy corresponding to equal densities in each habitat replicate. The slopes of the landscape generated for covered trays are much steeper than those generated for open trays (Fig. 7; please note the differences in scale).

Invasion landscapes from time available after foraging

Again, both invasion landscapes (Fig. 8) sink and change shape with vole density. The gain in 'fitness' attainable by an individual choosing the habitat with lower density increases dramatically with population size. But the shape of the landscapes depends on the fitness surrogate and how it is calculated. There is little gain in the time available for additional activities through habitat selection at low population sizes when voles face restricted foraging (Fig. 8A). If most individuals occupy one or the other habitat at high density, however, then an individual moving to the alternative habitat can reap a substantial gain in the time it has available to enhance fitness. Conversely, habitat selection yields reasonable increases in time at all population sizes for a new vole that shares foraging opportunities equally with residents throughout the habitat (Fig. 8B).

DISCUSSION

To the extent that foraging behaviours are adaptive it should be possible, with appropriate caution (e.g. Fawcett *et al.*, 2013), to co-opt them as surrogates for fitness to solve otherwise difficult eco-evolutionary problems. This view is supported by the foraging behaviour of

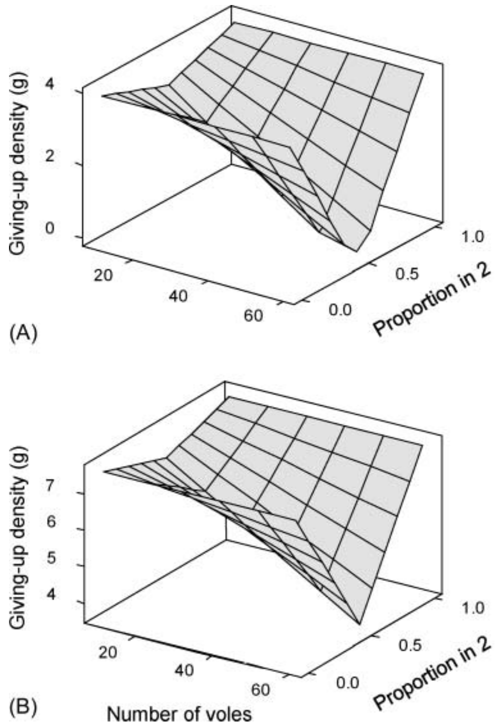

Fig. 7. Invasion landscapes based on mean giving-up densities of meadow voles foraging in covered (A) and open (B) trays in enclosures at the Lakehead University Habitron, northern Ontario, Canada. Note the differences in scale.

meadow voles. Patterns of density-dependent foraging did reflect the equal opportunities provided by identical habitats. All landscapes correctly predicted a behaviourally (Giraldeau and Dubois, 2008) and evolutionarily stable equilibrium (ESS) at which an equal number of individuals should occupy each habitat.

Despite the same equilibrium solutions, the topography of the landscapes depended on which surrogate I used for fitness. The habitat-selection landscape is mostly flat across a moderate range of densities when we assume that individuals begin foraging at the current quitting-harvest rate (QHR; Fig. 8A). Neither behaviour nor habitat selection shows much advantage towards equal occupation of both habitats in the 'flat zone'. But the landscape changes dramatically at higher densities. Large departures from the ESS (when most individuals occupy one or the other habitat) yield huge dividends for individuals that disperse to the alternative habitat. If immigrants or recruits share resources equally with residents, however (Fig. 7 and Fig. 8B), then dispersal in these V-shaped landscapes is favoured for all non-ESS strategies at all densities.

No doubt such rewards play a major role in density-dependent habitat selection by voles (Pusenius and Schmidt, 2002; Lin and Batzli, 2004; Oatway and Morris, 2007; Morris and MacEachern, 2010) and numerous other species. What is most important, however, is that at high densities even small departures from the ESS can create large opportunities for those individuals that move to the alternative habitat. The lesson revealed here sheds light on the oft-heard

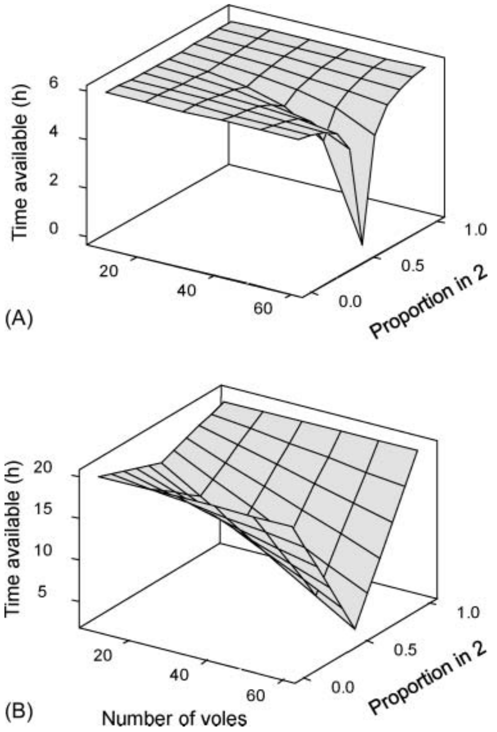

Fig. 8. The invasion landscapes of time available for fitness-enhancing activities by meadow voles in the Lakehead University Habitron, northern Ontario, Canada. (A) Estimate for an additional vole foraging in trays, and which commences foraging at the quitting-harvest rate. (B) Estimate for an additional vole that forages throughout the habitat and achieves harvest rates equal to residents. Note the differences in scale.

statement that habitat preferences emerge most clearly at low population densities. When density is low, dispersal by a few individuals can alter the proportion living in each habitat dramatically with negligible effects on fitness. When density is high, however, the same strategy of habitat selection (the same proportion in each habitat) can be attained only by dispersal of many individuals with large cumulative effects on fitness. Whether habitat preference is most easily observed at low or high densities thus depends on the topography of the invasion landscape and on the connection between fitness and the behaviours responsible for habitat choice.

The two landscapes in Fig. 8 represent the extremes of a continuum that correspond roughly with contest (interference) and scramble (exploitation) competition (Nicholson, 1954). The intriguing outcome is that habitat selection is likely to be less pronounced at low density when resident individuals restrict foraging by newcomers (Fig. 8A) than it is when all individuals compete equally (Fig. 7 and Fig. 8B). Those differences suggest that it may be possible to infer the form of intraspecific competition from the pattern of habitat selection and vice versa.

The valley floor of the invasion landscape represents the proportional occupation of habitat emerging from the habitat isodar. Departures on either side correspond with the residuals that one might find in an isodar regression. Imagine that the ESS proportion of individuals occupying a habitat is constant. The magnitudes of residuals about the isodar for that constant strategy necessarily increase with population size. But the advantage to an individual of moving from the high-density habitat to the low-density one for a given non-ESS strategy also increases with population size. We thus expect, in these V-shaped landscapes, a gradual diminution of isodar residuals with increasing population size.

Isodar residuals emanating from restricted foraging, as illustrated in Fig. 8A, should instead be greater at low densities where habitat selection yields minimal returns. Those residuals will undergo a rapid constriction at higher densities.

Oatway and Morris (2007, their Figure 2, p. 484) constructed isodars for meadow voles occupying two of the same paired enclosures I use here. With only 11 data points, their data are too coarse to definitively confirm one model of intraspecific competition over another. Nevertheless, there is no obvious constriction in residual variation about the isodar that would signify restricted foraging opportunities. It thus appears that voles in the Habitron attain equal foraging opportunities and that their invasion landscapes might be easily generated from data on population density and giving-up density (GUD). If such ability is widespread, then it could assist attempts to conserve low-density remnant populations of cryptic species where alternative fitness estimates and direct observations are either difficult or impossible.

Our confidence in a V-shaped landscape for meadow voles, and its rapid construction with GUDs or QHRs as surrogates, would be increased if other fitness metrics for meadow voles exhibit similar linear density dependence. Supporting evidence for this conjecture is found in Lin and Batzli's (2001) ambitious study measuring population growth rates, recruitment, and dispersal by meadow and prairie voles in enclosures similar to those in the Habitron. Population growth rates and net recruitment during the reproductive season declined linearly as the density of meadow voles increased. It is inconceivable, nevertheless, that vole population dynamics would respond instantly to changes in density. Fitness estimates must necessarily include seasonal, and perhaps longer, time lags. Such long time lags are unlikely for fitness surrogates based on foraging behaviour. Behaviours may thus yield more reliable invasion landscapes than those based on life-history or population-derived fitness assays.

Some might question whether behavioural surrogates should be restricted to solving games involving behaviourally stable strategies [BSS (Giraldeau and Dubois, 2008)] rather than evolutionary stability. The answer hinges on the reliability of the behavioural gambit (Giraldeau and Dubois, 2008; Fawcett *et al.*, 2013) where cognitive processes can at least partially disconnect behaviour from fitness. An individual's allocation of foraging time to different types of patches, as might be revealed by GUDs, must surely emerge through a variety of proximate cognitive mechanisms. Landscapes built with foraging behaviour are then best thought of as the individual's BSS. But income breeders (Thomas, 1988), such as voles, are capable of successful reproduction only if they can harvest energy in excess of their maintenance requirements. Fitness emerges in such organisms through efficient harvest of that 'surplus' energy. Time-specific assessment of foraging behaviour, including GUDs and QHRs, should thus represent reliable surrogates with which to assess both the BSS and ESS.

Scientists who use foraging metrics to evaluate behaviourally and evolutionarily stable strategies should be on the alert for differences in energetic state that alter trade-offs between food and safety (e.g. Brown, 1988; Brown *et al.*, 1997; Lima and Bednekoff, 1999; Brown and Kotler, 2004). Energetic states can, for example, create different patterns in GUD beyond carrying capacity than at lower population sizes (Morris and Mukherjee, 2007). Researchers using foraging metrics should scrutinize any density-dependent variation in their data rather than assume that those data represent one consistent pattern with population density.

Nevertheless, invasion landscapes based on foraging behaviour overcome many of the reported problems associated with other fitness proxies and surrogates (e.g. Hunt and Hodgson, 2010). Unlike some surrogates, which lack ecological context (Gordon, 2011), foraging behaviour explicitly incorporates habitat similarities and differences in density and frequency dependence. It is encouraging that landscapes constructed from GUDs, the simplest of the three metrics, appeared as effective at revealing the strategy of habitat selection as the more complicated surrogates. Even so, future work should aim to evaluate the costs, benefits, and reliability of different foraging metrics. We also need experiments that evaluate the connection of behaviours with ostensibly more direct fitness estimates obtained from differential fecundity and survival. While we await the results of those experiments, rapid human-induced changes in habitat quality are likely to continue unabated. Our ability to predict the consequences of those changes depends heavily on developing leading indicators of ecological and evolutionary adjustments. The rapidity and reliability of adaptive behaviours suggests that we not only explore foraging surrogates for fitness, but also that we apply them widely to burgeoning problems of environmental change and reorganizing biodiversity.

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