



Competitive tragedies, habitat selection, and extinction (or not?)

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ABSTRACT

Background: Increasing competitive ability of individuals can create a Tragedy of the Commons ending in extinction. Theory has not yet evaluated what role adaptive habitat selection might play in the tragedy and its outcome.

Methods: We used modified Ricker population models to simulate the long-term population dynamics emerging from a pure strategy of despotic habitat choice versus a mixed strategy of despotic and ideal-free habitat selection. Density in the better of two habitats was reduced by the threat of dominance in the pure strategy. Habitat selection switched to an ideal-free distribution at low densities in the mixed strategy. We used patterns of density and dispersal, giving-up densities, personalities and condition of meadow voles to search for the predicted switch in habitat selection.

Results: Extinction probabilities in simulated stochastic environments were always higher for pure than for mixed strategies. Experiments on meadow voles were only partially consistent with a density-dependent transition from ideal-free to despotic habitat selection. Densities and giving-up densities of voles in adjacent habitats were nearly identical when resources were equal and population size was small. Giving-up densities diverged dramatically when supplemental food was added to one habitat and not to the other. Despite biased dispersal from high- to low-quality habitat, there was no associated difference in population density, personality or body condition.

Conclusions: Pure habitat selection based on dominance places populations at greater risk of extinction than does a mixed strategy in which dominance disappears at low population sizes. Experiments on meadow voles yielded limited but nevertheless tantalizing support for such a density-dependent switch in habitat selection.

Keywords: adaptation, extinction, foraging behaviour, habitat selection, *Microtus pennsylvanicus*, patch use, Tragedy of the Commons.

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INTRODUCTION

Competitive interactions among individuals can often lead to a Tragedy of the Commons (Hardin, 1968), whereby the increased fitness achieved by competitively dominant individuals reduces the overall population growth rate. Although a variety of mechanisms can rescue these populations (Gonzalez *et al.*, 2013; Carlson *et al.*, 2014), runaway evolution on competitive ability can reduce densities to levels where demographic or environmental stochasticity causes extinction (Matsuda and Abrams, 1994; Dercole *et al.*, 2002; Dieckmann and Ferrière, 2004; Greenman *et al.*, 2005). Evolution of traits adaptive to individuals can also yield invading mutant strategies that cause both the resident and mutant strategies to decline rapidly to zero – evolutionary suicide (Gyllenberg and Parvinen, 2001; Parvinen, 2005; Ferrière and Legendre, 2013).

Population declines are associated with the panoply of ecological and evolutionary events that influence population dynamics in addition to adaptive evolutionary suicide. These include density-dependent exploitation of resources, time-lags, food-web interactions, and deteriorating habitat quality. Each process can be expected to take place in heterogeneous environments where habitat selection can have dramatic effects on population dynamics and evolution (Holt, 1996, 2011; Morris, 2003, 2011a). The population dynamic and evolutionary consequences depend on the form of habitat selection and dispersal, species interactions, differences among habitats, and stochastic changes in population size and habitat quality (e.g. Holt, 1987; Morris, 1988, 2004, 2011b; Kawecki and Holt, 2002; Holt and Barfield, 2008, 2009; Morris and MacEachern, 2013; Kubisch *et al.*, 2014).

The dynamics associated with habitat selection are typically modelled as two extremes of a continuum where individuals are either free to occupy the habitat they choose [ideal-free (Fretwell and Lucas, 1969)] or are restricted in doing so by the behaviour of dominant individuals [despotic and pre-emptive habitat use (Fretwell and Lucas, 1969; Pulliam, 1988; Pulliam and Danielson, 1991; Rodenhouse *et al.*, 1997; McPeck *et al.*, 2001)]. These extremes appear to oversimplify habitat selection in real and simulated populations. Pusenius and Schmidt's (2002) field-enclosure experiments with meadow voles (*Microtus pennsylvanicus*) in New York State revealed both ideal-free and ideal-despotic habitat choice. The density and foraging success of animals choosing between risky mowed patches with or without supplemental food obeyed an ideal-free distribution (IFD). Animals choosing between safe unmowed patches with and without extra food lived at high density and fit an ideal-despotic distribution (IDD).

Very similar experiments conducted earlier with meadow voles in Illinois by Lin and Batzli (2001) yielded only ideal-free habitat selection, but over a longer time period (11 months) and across a range of densities (46 voles per hectare to approximately 550 voles per hectare in the best patches) less than the mid-autumn (October–November) populations used by Pusenius and Schmidt (2002) (i.e. >800 voles per hectare in favourable habitat). Oatway and Morris (2007) also observed ideal-free distributions in experiments on meadow voles living at low density (≤ 11 voles per hectare). These various experiments are consistent with computer simulations demonstrating that despotic and pre-emptive strategies are likely to co-exist in stochastic environments (Morris and MacEachern, 2013), and that the ordering of geometric mean fitness among strategies depends on population size (MacEachern, 2010).

It is thus possible, in declining populations, that a shift in habitat-selection strategy from dominance to free choice (and vice versa during population increase) might provide a mechanism that rescues populations from extinction by curtailing runaway selection towards ever increasing competitive asymmetry. We explore this possibility by using





simple models of single-species population growth in stochastic environments to evaluate differences in density-dependent fitness for a mixed ideal-free and ideal-despotic strategy versus pure despotic habitat selectors. The models mimic a field experiment with meadow voles designed to demonstrate whether voles occupying two identical habitats change from an ideal-free distribution to despotism when one habitat is made much more valuable than the other. A third alternative is that differences in competitive weights between habitats could produce a truncated phenotype distribution (Milinski and Parker, 1991) in which each habitat contains animals that differ in competitive abilities. We explore this third possibility by searching for differences between habitats in voles' mean body size, body condition, and personality (Sih *et al.*, 2004; Martin and Réale, 2007; Réale *et al.*, 2007). We conclude by discussing the implications of mixed habitat-selection strategies for our understanding of adaptive extinction.

THEORETICAL CONTEXT

Consider two identical habitats shared by a population growing according to Ricker's (1958) equation:

$$N_{i(t+1)} = N_{i(t)} e^{r_i \left(1 - \frac{N_{i(t)}}{K_i}\right)}$$

$$W_i = \ln(N_{i(t+1)}) - \ln(N_{i(t)}) = r_i - \frac{r_i N_{i(t)}}{K_i}, \quad (1)$$

where N is the density of individuals in habitat i , r is the instantaneous rate of population growth, K is the habitats' carrying capacity, and W (the difference in the logarithms of density) represents fitness. We wish to explore the conditions under which an ideal-despotic distribution can yield higher fitness for dominant individuals than does an ideal-free distribution. To do so, we imagine that the occupation of the two habitats is determined by the movement of subordinate individuals making an ideal choice of habitats in which they perceive that fitness has been degraded by density-independent costs of dominance, such as that associated with acquiring and defending territory (Fretwell and Lucas, 1969):

$$W'_1 = (r_1 - \Delta_1) - \frac{(r_1 - \Delta_1)N_1}{K_1 - \partial_1}$$

and

$$W'_2 = (r_2 - \Delta_2) - \frac{(r_2 - \Delta_2)N_2}{K_2 - \partial_2}$$

where W'_i is the perceived fitness in habitat i (e.g. Fretwell and Lucas, 1969), and Δ_i and ∂_i represent the perception, respectively, that dominant individuals have reduced the maximum population growth rate and carrying capacity.

Thus at equilibrium ($W'_1 = W'_2$),

$$N_2 = \left(\frac{(r_2 - \Delta_2) - (r_1 - \Delta_1)}{(r_2 - \Delta_2)} \right) (K_2 - \partial_2) + \left(\frac{(r_1 - \Delta_1)(K_2 - \partial_2)}{(r_2 - \Delta_2)(K_1 - \partial_1)} \right) N_1 \quad (2)$$





specifies the isodar (Morris, 1988), the densities of individuals in each habitat such that fitness is the same in each. For simplicity, we imagine that Δ and ∂ represent reductions only in the fitness perceived by subordinate individuals, and not an absolute reduction in population growth rate. Under these assumptions, dominant individuals will achieve higher fitness in habitat 2 only if the density there with despotic behaviour is less than it would be with ideal-free behaviour, that is, only if

$$\frac{(r_2 - r_1) K_2}{r_2} + \left(\frac{r_1 K_2}{r_2 K_1} \right) N_1 > \left(\frac{(r_2 - \Delta_2) - (r_1 - \Delta_1)}{(r_2 - \Delta_2)} \right) (K_2 - \partial_2) + \left(\frac{(r_1 - \Delta_1) (K_2 - \partial_2)}{(r_2 - \Delta_2) (K_1 - \partial_1)} \right) N_1.$$

Whether the inequality is true depends on the relationships and relative differences in Δ and ∂ between the two habitats (Fig. 1). The main point is that there are conditions under which it is reasonable to assume that ideal-free habitat selection over one range of densities might be displaced by ideal-despotic habitat selection at some other range, and vice versa. Systems where the IFD yields higher fitness than the IDD at low population sizes might thereby be rescued from escalating asymmetric competition associated with runaway selection on dominant behaviour. Rescue will be enhanced if populations switching between strategies at low density also tend to be more stable than those with only ideal-despotic habitat selection.

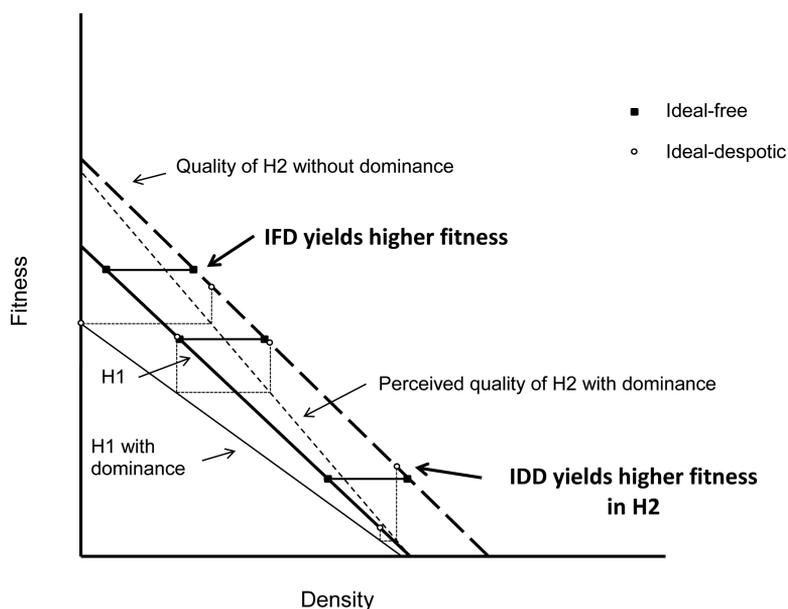


Fig. 1. An example showing conditions under which an IFD can yield higher fitness at low density when an IDD yields higher fitness in high-quality habitat at high density. Negatively sloped lines indicate the actual and perceived density-dependent decline in fitness in two habitats (H1, solid lines; H2, dashed lines). Bold horizontal lines and solid squares indicate fitness when habitat selection is ideal free. Dotted horizontal and vertical lines with open circles indicate the fitness in both habitats, at the same population size as the IFD, assuming that habitat choice is based on the perceived fitness in each habitat. The cost of dominance devalues the perception of fitness by habitat selectors in each habitat. The value of the respective strategies depends critically on habitat quality and the cost associated with dominance.





METHODS

Population stability

We simulated population dynamics for hypothetical semelparous asexual populations in which fitness declined linearly with increasing density. The sequence of operations was population growth according to each habitat's density-dependent per capita growth rate followed by dispersal according to either the ideal-free or ideal-despotic distribution. We modified carrying capacity in each generation as $K' = \alpha K$, where α is a proportion (in units of 0.1 or 0.01) drawn at random from a uniform distribution. Data collection began after we seeded each habitat with four individuals and allowed them to select habitat and grow for 500 generations.

In models such as Ricker's equation (1), N represents population density. At the scale of our simulations, we instead consider N as the number of individuals and assume that demographic stochasticity is sufficiently small that the dynamics follow (1). We imagined that partial individuals would not survive, so we rounded population sizes at the end of each generation down to the nearest integer (individual). Extinction thus occurred whenever $N < 1$. We extracted population sizes and mean growth rates from the following 100 generations, and counted all extinction events. We repeated the entire process 1000 times before iterating parameter values. We restricted our interest to populations with high growth rates because slowly growing populations should, except for stochastic effects, grow asymptotically to their carrying capacities. These populations would not be subject to the catastrophic declines in populations where high growth rates cause density to overshoot K . Our focus is extinction, so we restricted sensitivity analyses to a subset of parameter values where there were major differences in extinction probabilities between the two habitat-selection strategies.

We used Ricker's equation to determine population growth when individuals chose between habitats based on the IFD, and a modified version of equation (2) in which dominant individuals altered the perception of fitness (W'_i , the apparent value used by individuals seeking to occupy that habitat) in proportion to density, only in habitat 2. We used this simpler version because it better represented our habitat-scale manipulation of quality in only one of two habitats (described under 'Field experiment' below). The perceived fitness did not affect the actual fitness achieved by individuals living in that habitat. The model thus assumes, as does the original by Fretwell and Lucas (1969), that territorial or competitively dominant individuals choosing the high-quality habitat repel potential new occupants with negligible cost to their own fitness. Doing so guarantees lower density in the high-quality habitat than occurs with the IFD and exacerbates the risk of extinction in that habitat associated with stochastic variation in carrying capacity. Overall dynamics, but not necessarily patterns in mean fitness, would be similar if we used a more complicated model such as that depicted in Fig. 1.

The Tragedy of the Commons in our simulation occurs through the suboptimal allocation of individuals between habitats (e.g. Morris *et al.*, 2001) rather than through wasted resources. Thus, for the IDD,

$$W'_2 = r_2 - \frac{r_2}{K'_2} N_2 - (\Delta'_2 + b_2 N_2), \quad (3)$$

where Δ' represents a baseline reduction in the perception of fitness caused by dominance, b is the density-dependent increase in the cost of habitat choice, and K' indicates that





carrying capacity is subject to stochastic variation. We calculated the expected IFD density by re-ordering the isodar for habitat 2:

$$N_2 = \frac{(r_2 - r_1)K'_2}{r_2} + \left(\frac{r_1 K'_2}{r_2 K'_1}\right) N_1. \quad (4)$$

Letting $N_1 + N_2 = TOTN$ and substituting for N_2 ,

$$N_1 = \frac{TOTN - \left(\frac{r_2 - r_1}{r_2}\right) K'_2}{1 + \left(\frac{r_1 K'_2}{r_2 K'_1}\right)}. \quad (5)$$

The rearrangement eliminates problems associated with simultaneously calculating the equilibrium density in two habitats. In the case of the density-dependent cost of dominance, we assumed that the perceived value of habitat 2 was associated with the density of individuals living there after reproduction but before dispersal, and thus calculated the expected density with dominance as

$$N_1 = \frac{TOTN - \left(\frac{r_2 - r_1}{r_2}\right) K'_2 + \left(\frac{K'_2}{r_2}\right) (\Delta'_2 + b_2 N_2)}{1 + \left(\frac{r_1 K'_2}{r_2 K'_1}\right)}. \quad (6)$$

We invoked equation (5) only when total population density was less than a threshold proportion of the summed carrying capacities in the two habitats. Thus, when the combined density was high, individuals selected habitat according to despotic habitat choice (eq. 6), and when the combined density was below the threshold, habitat selection switched to ideal-free choice (eq. 5). We then compared extinction rates generated by this mixed habitat-selection strategy with that generated by despotic habitat selection alone.

Field experiment

We manipulated habitat quality in two pairs of adjacent 50 m × 50 m field enclosures surrounded by a 0.75 m rodent-proof galvanized metal fence at the Lakehead University Habitron (www.evolutionary-ecology.com/data/2977Appendix.pdf, Fig. A1, E1 paired with E3; E2 paired with E4). Two equidistant ground-level gates (9.25 cm diameter) allowed voles to move from one enclosure to the other. Enclosures contained old-field habitat intermixed with rapidly growing red pine (*Pinus resinosa*; 3–5 m tall).

We closed the gates and removed all small mammals with single live traps placed at each of 16 stations in each enclosure (12.5 m grid spacing) for three consecutive nights in late May 2014, and again in early June. We then added three male and three female voles to two of the enclosures, and six males and six females to a third enclosure on 14 June (E2; [2977Appendix](http://www.evolutionary-ecology.com/data/2977Appendix.pdf), Fig. A1). The fourth enclosure (E4) remained empty until 21 June when gates were opened between that enclosure and the one containing 12 voles. Doing so





ensured that any subsequent similarity in densities would necessarily be caused by dispersal. We confirmed dispersal with images from an infrared-detecting camera (model PC90, Reconyx, Holmen, Wisconsin) positioned at each open gate.

We placed four pairs (safe and risky) of plastic 'bell-pot' foraging trays (40 cm diameter) in the shade of a red pine tree at the four corner trapping stations in each enclosure. We protected each tray from wind and rain with a 60 cm × 60 cm × 14 cm wooden frame covered either by a clear polyethylene sheet (open = risky) or plywood (cover = safe). We placed copious amounts of striped sunflower seed and alfalfa cubes in each tray, and resupplied as needed, so that voles would have adequate food and be accustomed to foraging in trays when the experiment began.

We closed the gates on 28 July and initiated a three-day weekly regimen of broadcasting striped sunflower seed at the four internal stations of two of the enclosures. We used estimates from Morris and MacEachern (2010) and Morris (2014) in order to allocate enough food to fulfil the metabolic requirements of all voles occupying the two enclosures until the next regularly scheduled feeding period. We maintained a running tally on voles known alive with twice-weekly (Wednesday and Friday) live trapping. We avoided competition for access to traps by allocating at least twice as many live traps to an enclosure as there were voles (2–5 traps at each station).

We mixed 8 g of whole oats in 1.5 litres of sieved silica sand, and poured the mixture into the foraging trays at 16:00 h each Monday and Wednesday (= days 1 and 2) for five consecutive weeks. We collected the trays 22 hours later, sieved the sand, and weighed the remaining oats to determine each tray's giving-up density (GUD). Giving-up densities are closely related to quitting-harvest rates and can be used to infer patterns in predation risk when collected in pairs of safe versus dangerous patches (Brown, 1988; Brown and Kotler, 2004; Morris, 2014, and many more). We replaced trays containing the oat–sand mixture with empty trays during all intervening days (including weekends). We repeated the full regimen for five consecutive weeks until 29 August.

Animal personalities and condition index

We used modified hole-board and novel-object field tests (Martin and Réale, 2007) to evaluate vole personalities. We placed single voles into a plastic open-field box with four symmetrically located 1.9 cm diameter holes in the floor. We recorded the movements and behaviour of each vole with a video camera (GoPro Hero 3) for 5 minutes. We then placed a metal thumb-counter at one end of the arena and recorded the vole's reaction to the novel object for a further 5 minutes. We displayed the videos on a computer monitor so as to measure a series of variables expressing movement and curiosity.

We measured seven personality variables on 190 voles during the field season (2977Appendix, Table A1). Twenty-four of these animals comprised the initial cohort of introduced voles. Beginning on 29 July, we chose one adult male and one non-lactating adult female vole at random from each enclosure during each trapping day for additional personality assays (98 animals in total; the remainder were assayed in the context of other experiments). We did not systematically expose animals to repeated trials required to reveal consistent responses of individuals over time or in different circumstances (e.g. Martin and Réale, 2007; Réale *et al.*, 2007). We thus caution readers that our use of the term 'personalities' refers to patterns revealed by covariation among traits rather than repeated measures of those traits on individual animals.





We used only adult males in our assessment of animal condition. We searched the data for the maximum length (mm) measurement associated with each animal, used it to predict the body mass observed on that day (least-squares linear regression), and calculated the residuals from the regression as the unbiased estimate of body condition (Schulte-Hostedde *et al.*, 2001, 2005).

Statistical analysis

We searched for differences in the minimum number of voles known alive (MNKA) in enclosures through time with stepwise multiple regression. We included a quadratic term to represent density-dependent declines in growth rates and represented different enclosures with indicator variables (with E4 as the comparison standard). The minimum number alive is an appropriate estimate of abundance for these enclosed populations because all trapping procedures were identical among enclosures, recapture rates were high (e.g. all 61 animals captured in the first night of trapping were recaptured subsequently, only 1 of 74 animals captured in the second night failed to be captured two or more times), and it allowed us to adjust estimates for marked individuals dispersing between E2 and E4. We used mixed-model repeated-measures GLMs to assess temporal-spatial variation in giving-up densities [fixed effects = tray (cover vs. open), enclosure, day (GUDs collected on Tuesday vs. Thursday), and week; random effect = stations nested within enclosures; covariance structures = identity for station and AR(1) for repeated measures]. We chose the model with the lowest AIC [and with $\Delta\text{AIC} > 2$ (Burnham and Anderson, 2002)] as the most parsimonious fit with the data.

We summarized animal personalities with varimax rotated principal components analysis (PCA) and used the broken-stick rule (Peres-Neto *et al.*, 2005) to determine the number of informative PCs. We then used a multivariate GLM to search for differences in personality scores among enclosures, between the sexes, and their interaction. We used a univariate GLM to assess differences among enclosures in the residuals (body condition) from linear regressions of body mass versus maximum length. We repeated the analysis using only body length and completed our assessments with contingency analyses evaluating differences in dispersal between E2 and E4, as well as differences in sex ratios among the enclosures. We conducted all analyses in SPSS v.22 and MINITAB v.17.

RESULTS

Computer simulations

The relative stability of simulated populations selecting habitat according to mixed versus ideal-despotic distributions depended on parameter values. Both strategies of habitat selection caused high rates of extinction in highly stochastic environments (Fig. 2). When stochastic variation in carrying capacity was reduced, however, the probability of extinction was consistently lower for the mixed strategy of habitat choice. Extinction rates also depended on the threshold population size at which the strategies changed (Fig. 3A) but the rates were lower for higher costs of dominance ('Delta' = Δ' ; relatively more individuals forced into the poorer habitat at high population sizes).

Pure and mixed strategies were also at high risk of extinction when the carrying capacity of the poor habitat was low (Fig. 3B). A poor habitat with a low carrying capacity could



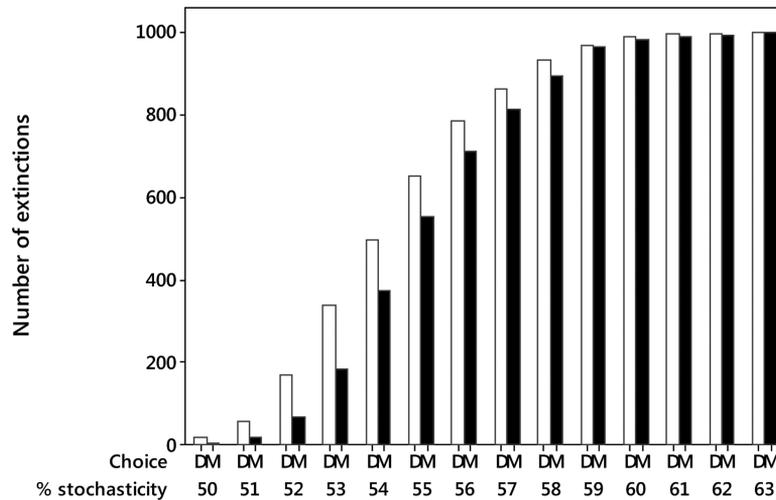


Fig. 2. The number of extinctions in computer simulations of mixed (M, ■) and ideal-despotic (D, □) selection between two habitats. Parameter values: $r_2 = 2.75$, $r_1 = 2$, $K_2 = 200$, $K_1 = 90$, $\Delta' = 1.2$, $b = 0.001$, threshold for mixed = 0.5. Percent stochasticity = $a \times 100$.

absorb too few individuals produced in the larger high-quality ‘source’. Even so, the mixed strategy retained a lower risk of extinction with increasing carrying capacity than did IDD populations (Fig. 3B).

Both types of distributions yielded increased risk of extinction at moderate levels of density-independent costs (Δ' ; Fig. 4A). Extinction rates declined in simulations that increased the density-dependent costs of habitat selection (Fig. 4B). In both cases, the risk of extinction was far less for the mixed strategy than for pure despotic habitat selection. All simulations thus revealed a consistent and convincing pattern in which the mixed strategy buffered populations against extinction.

Field experiment

Vole populations increased more than five-fold during the experiment (from the 24 original animals to 137 known alive at the end of the experiment). The pattern of density through time depended on enclosure ($F_{4,35} = 67.6$, $P < 0.001$; Table 1, Fig. 5). Vole abundance diverged significantly between control enclosures (E1 and E3), and was similar between experimental enclosures. Even so, it is intriguing that the density in E4 appeared to lie below that in E2 at the beginning of the experiment but higher at the end (Fig. 5B).

Mean giving-up densities were lower under cover (safety) than in the open ($F_{1,57.2} = 104.09$, $P < 0.001$), lower in enclosure E3 than E4, and lower in both E3 and E4 than in E1 and E2 ($F_{3,10.6} = 30.24$, $P < 0.001$; pairwise contrasts; Table 2, Fig. 6). Mean giving-up densities were also lower on day 1 than on day 2 ($F_{1,77.5} = 30.51$, $P < 0.001$), and varied among weeks ($F_{4,59.6} = 7.96$, $P < 0.001$; week 3 less than weeks 1 and 2, weeks 4 and 5 less than weeks 1–3, pairwise contrasts; Table 2, Fig. 6). Mean differences in giving-up densities between trays depended on which enclosures were contrasted [lowest in E3 at 0.36 g, similar in E1 (1.83 g), E2 (1.96 g), and E4 (2.32 g): $F_{3,57.2} = 7.38$, $P < 0.001$] while



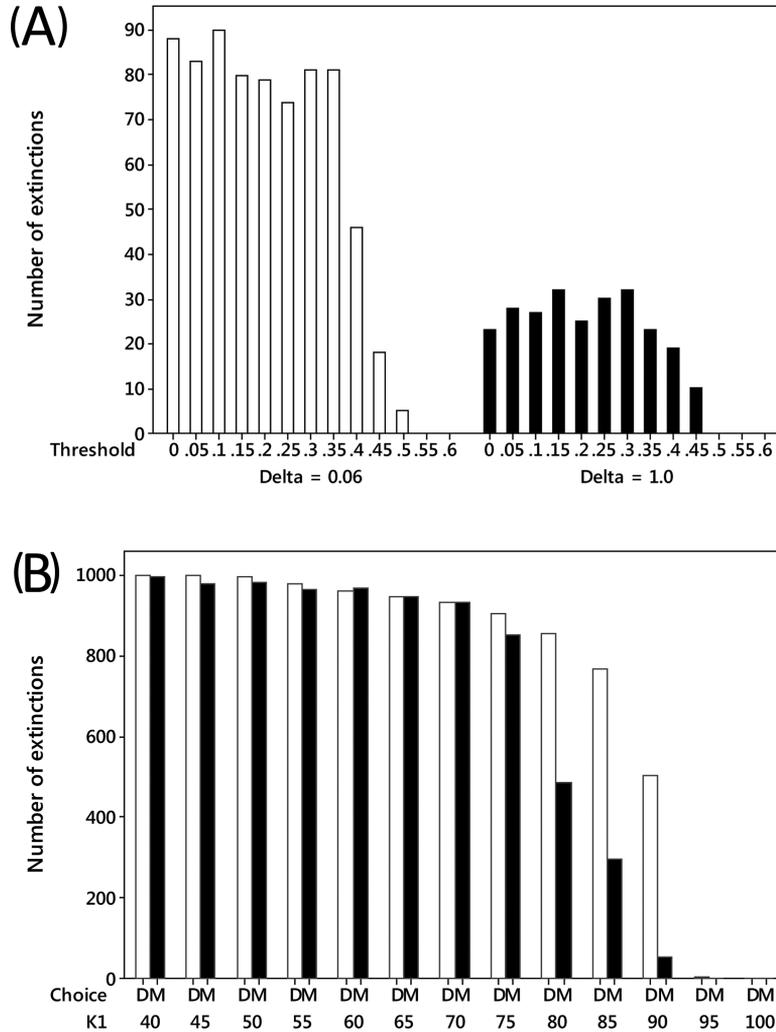


Fig. 3. The effects of the threshold density below which ideal-free habitat selection occurred and variation in carrying capacity on extinction rates of habitat selectors in computer simulations. D = despotic habitat selection, M = combination with ideal-free; changes in the threshold apply only to populations combining ideal-free habitat selection at low density with despotic habitat selection at higher densities. Parameter values as follows: $r_2 = 2.75$, $r_1 = 2$, $K_2 = 200$, $K_1 = 100$; panel (A): $b = 0.0006$, stochastic variation = 0.5 in units of 0.01; panel (B): $\Delta' = 1.2$, $b = 0.0012$, stochastic variation = 0.5 in units of 0.1 respectively.

differences among enclosures depended on which weeks were compared ($F_{12,59,6} = 12.5$, $P < 0.001$ and $F_{19,54,3} = 1.80$, $P = 0.046$ respectively for the two-way and three-way interactions; Table 2, Fig. 6). These results are consistent with state-dependent foraging decisions based on differences in safety between trays, differences between enclosures with supplemental food and those without, changes in individuals' state through time, and differences among animals that could disperse and those that could not.





Extinction via habitat selection

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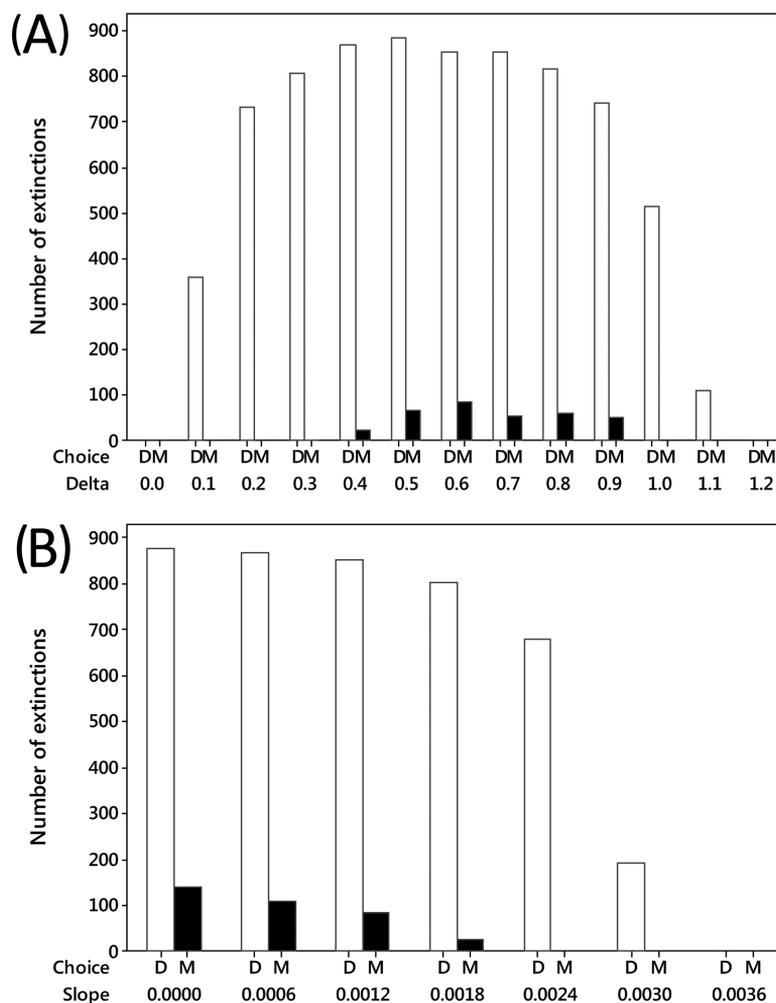


Fig. 4. Extinction rates of despotic (D, \square) and mixed (M, \blacksquare) habitat selectors with variation in the density-independent (Δ') and density-dependent (slope = b) costs of despotic behaviour. Parameter values as follows: $r_2 = 2.75$, $r_1 = 2$, $K_2 = 200$, $K_1 = 100$, stochastic variation = 0.5 in units of 0.1 with $b = 0.001$ (panel A) and $\Delta' = 0.6$ (panel B) respectively.

Two principal components (PCs) accounting for approximately 55% of the common variation in behaviour satisfied the broken-stick criterion for informative personality axes (2977Appendix, Table A1). The first component scaled behaviour from active voles with high scores on all activity variables [often considered an index of boldness (Toms *et al.*, 2010; but see Réale *et al.*, 2007; Dall and Griffith, 2014)] to mostly inactive animals with relatively high scores on grooming behaviour. PC2 represented a cline from highly vigilant animals with high scores on scanning and sniffing behaviours with little time spent grooming, to the opposite.

Ninety-eight animals with personality scores were distributed more-or-less equally among enclosures and between the sexes (2977Appendix, Table A2). Despite clearly defined





Table 1. Significant results from a stepwise multiple regression assessing patterns of vole abundance through time in two control (E1 and E3) and two treatment (E2 and E4) enclosures at the Lakehead University Habitron

Source	d.f.	<i>F</i>	<i>P</i>
Regression	1	67.6	<0.001
Census	1	76.4	<0.001
Census ²	1	32.2	<0.001
Indicator E1	1	4.8	0.035
Indicator E3	1	18.1	<0.001
Error	35		

Table 2. Summary of ‘the best’ repeated-measures mixed-model GLM assessing differences in mean GUDs of meadow voles foraging in safe and risky trays in different enclosures through time at the Lakehead University Habitron

Source	d.f.	<i>F</i>	<i>P</i>
Intercept	1,10.6	329.95	<0.001
Tray (open vs. cover)	1,57.2	104.09	<0.001
Enclosure	3,10.6	30.24	<0.001
Day (1 vs. 2)	1,77.5	30.51	<0.001
Week	4,59.6	7.96	<0.001
Tray × Enclosure	3,57.2	7.38	<0.001
Tray × Day	1,62.5	0.10	0.747
Tray × Week	4,60.3	2.23	0.309
Enclosure × Week	12,59.6	12.50	<0.001
Tray × Enclosure × Week	12,60.3	1.41	0.187
Enclosure × Day × Week	19,54.3	1.80	0.046
Four-way interaction	19,55.8	0.73	0.769

personality axes, there were no significant differences in the mean value of either PC among enclosures (PC1: $F_{3,90} = 1.11$, $P = 0.35$; PC2: $F_{3,90} = 0.77$, $P = 0.52$), between the sexes (PC1: $F_{1,90} = 0.53$, $P = 0.47$; PC2: $F_{1,90} = 0.03$, $P = 0.87$), or in the interaction between sex and enclosure (PC1: $F_{3,90} = 2.16$, $P = 0.098$; PC2: $F_{3,90} = 0.74$, $P = 0.53$).

Our analyses of differences in adult sex ratios among enclosures ($\chi^2 = 1.0$, d.f. = 3, $N = 170$, $P = 0.8$), and of differences in net dispersal from camera images ($\chi^2 = 4.77$, d.f. = 3, $N = 236$, $P = 0.19$) were both non-significant. Body mass was tightly linked to maximum body length of adult male voles (mass = $-34.7 + 0.59$ length; $F_{1,76} = 329.2$, $P < 0.001$, $R^2 = 0.81$) but there was no significant difference in body length ($F_{3,74} = 1.5$, $P = 0.22$), or in the residuals specifying body condition ($F_{3,74} = 0.9$, $P = 0.43$), among enclosures. We repeated the analysis using only animals captured on the final two days of the experiment (period 5) and obtained similarly non-significant results.



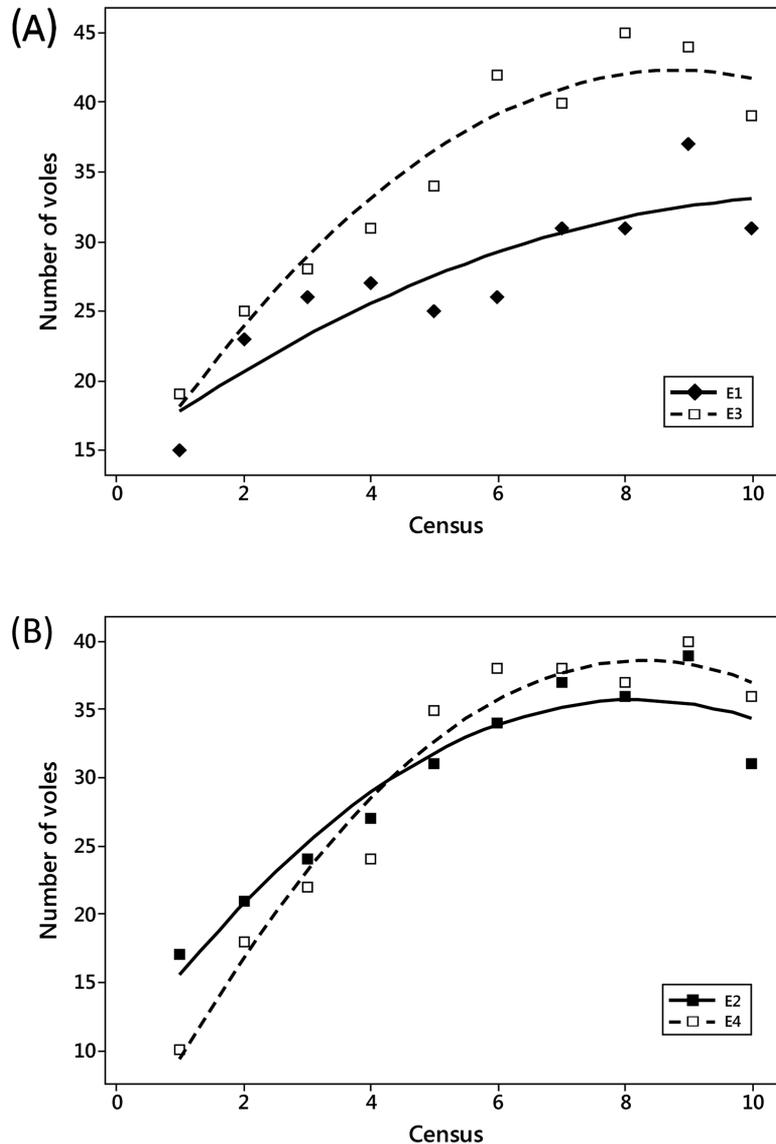


Fig. 5. The pattern of vole abundances through time (census periods) in two control (A: E1 and E3) and two treatment (B: E2 and E4) enclosures at the Lakehead University Habitron.

There was, however, a significant difference in the proportion of animals known to disperse from E2 to E4 (8 of 9) relative to those dispersing from E4 to E2 (1 of 9; $\chi^2 = 5.44$, $P = 0.02$). There was an equal difference in the sex ratios of dispersing animals (1 female: 8 males). But the mean personality scores of these nine animals for both PC1 and PC2 were not different from the population mean (0; one sample t -test: $t = 0.83$, $P = 0.43$ and $t = 0.45$, $P = 0.66$ respectively).



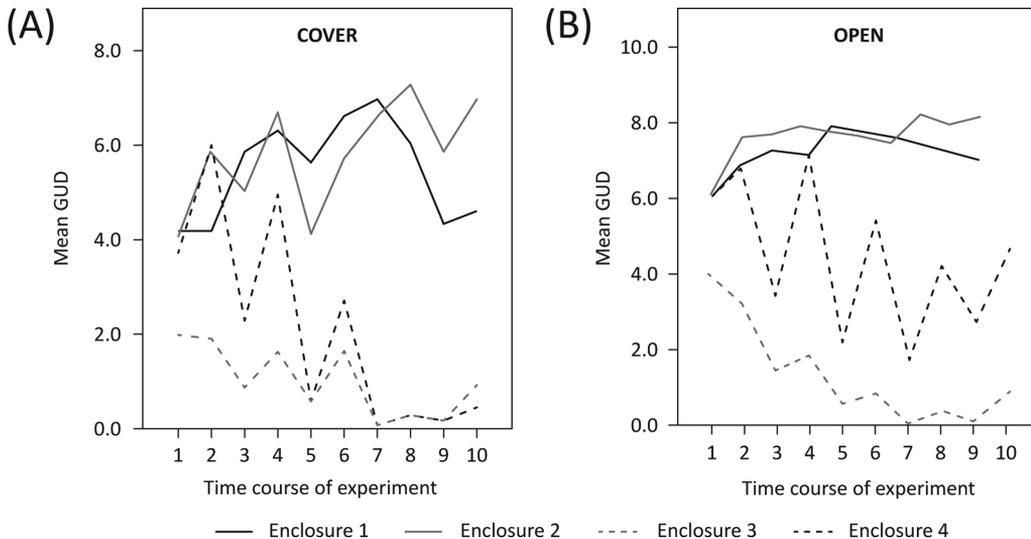


Fig. 6. Mean giving-up-densities (GUD) through time (A) under cover (= safe) and (B) in the open (= risky) in four field enclosures at the Lakehead University Habitron. Time course as follows: 1 and 2 = days 1 and 2 of week 1 (28 and 31 July); 3 and 4 = week 2 (5 and 7 August); 5 and 6 = week 3 (12 and 14 August); 7 and 8 = week 4 (19 and 21 August); 9 and 10 = week 5 (26 and 28 August). Please note differences in scale between panels (A) and (B).

DISCUSSION

Individuals living in a temporally variable environment with a mosaic of habitats can often improve their fitness by moving from one habitat to another. The net benefit depends not only on the fitness prospects of different habitats, but also on the costs associated with dispersal, establishing residence, and repelling intruders (e.g. Morris and MacEachern, 2013). Costs are most easily re-paid in high-quality habitats where competitive asymmetries in interference among individuals create differences in mean fitness that increase dispersal by subordinates towards lower-quality habitat alternatives (Fretwell and Lucas, 1969; Pulliam, 1988; Rodenhouse *et al.*, 1997; McPeck *et al.*, 2001; Morris and MacEachern, 2013). The value (and necessity) of interference is least at low density when fitness differences among habitats are minimized (Morris *et al.*, 2010; Morris, 2011a). It is thus reasonable to assume that many species might switch from an ideal-free distribution at low density to a despotic distribution at higher densities when fitness penalties of improper habitat choice outweigh the costs of despotism. The advantages of despotic behaviour would be enhanced in environments where the difference in mean habitat quality is greatest. Such interference can produce a Tragedy of the Commons whereby the fitness of all individuals is reduced, and the probability of extinction increased, relative to *laissez-faire* co-existence (Matsuda and Abrams, 1994; Dercole *et al.*, 2002; Dieckmann and Ferrière, 2004; Greenman *et al.*, 2005; Rankin *et al.*, 2007).

Our simulations revealed that despotic habitat selection, like other forms of asymmetrical competition, can indeed destabilize population dynamics to the point of extinction. The risk of extinction is reduced, however, when individuals switch to ideal-free habitat selection at low population sizes. Extinctions in our models emerge through time-lagged effects of





variation in carrying capacity. Populations that grow to high density when carrying capacity is also high can crash to extinction if carrying capacity is suddenly reduced. Despotic populations are more prone to this form of extinction because the reduced density of individuals in the better of the habitats can enable rapid population growth that overshoots carrying capacity.

When populations obey an ideal-free distribution, the sub-populations in each habitat grow at identical rates. Although such populations can and do overshoot carrying capacity, the growth rates in both habitats decay similarly with increasing population size. The probability of an overshoot and subsequent crash to extinction diminishes as the densities in each habitat simultaneously approach the summed carrying capacity in the environment. In contrast, growth rates are always higher in the richer of the two habitats when individuals follow an ideal-despotic distribution. With dominance, population growth remains positive in the better habitat even when the summed population size is equal to the summed K 's. If fewer individuals occupy poor habitat than live in the rich one, such populations will often be prone to further population increase and the potential for a subsequent catastrophic collapse. No such tragedy awaits ideal-free habitat selectors for which the net population growth, at the same density ($N_1 = K_1$; $N_2 = K_2$), would be zero.

The mixed strategy operates differently. In this strategy, ideal-free distributions exist only below a population-size threshold. Even so, relatively more individuals occupy the better habitat under the mixed strategy when population size is low than is the case for dominance. The higher density in the richer habitat at low population sizes dampens the oscillations in that habitat that precede extinction. In order to appreciate this effect, imagine logistic population growth in two habitats with parallel fitness functions and that habitat 2 (H2) has both a higher rate of increase and carrying capacity than does habitat 1 (H1). Let the current population size equal $(K_1 + K_2)/2$ and the effect of dominant individuals is to create densities of $K_1/2$ and $K_2/2$ in H1 and H2 respectively. The population would grow at its maximum rate but since H2 is superior to H1, the fitness of an individual in H2 at density $K_2/2$ is greater than that of an individual living in H1 at density $K_1/2$. Fitness can be equalized between the habitats (an IFD) only if the number of individuals in H2 exceeds $K_2/2$ (and those in H1 $< K_1/2$). Total population growth is necessarily less with this IFD than it was with dominance. Ideal-free habitat selection thus tends to dampen fluctuations that would otherwise occur under purely despotic habitat choice. This effect depends (1) on the relationship between fitness and density in each habitat (Fig. 7), and (2) on the ability of the poorer habitat to absorb dispersing individuals (e.g. Fig. 3b).

The buffering effect of the mixed strategy was most clearly revealed in simulations that varied the cost of dominance. When the cost was low, the IDD solution converged on that of the extinction-free mixed strategy (Fig. 4A). As the cost increased, a smaller proportion of individuals occupied the better habitat. That habitat's relatively high growth rate allowed the population to greatly overshoot carrying capacity and doom the descendants to extinction. But as the cost increased further, the effective growth rate in the increasingly low-density but high-quality habitat was reduced, enabling persistence. This important result implies that runaway selection for increased dominance does not necessarily create a collapsing Tragedy of the Commons (Rankin *et al.*, 2007), and particularly so in the case of density-dependent habitat selection. Such high costs of dominance might nevertheless require prolonged periods of relatively stable carrying capacities in order to pass through the high rates of extinction that otherwise occur with intermediate levels of cost (Fig. 4A). It thus seems reasonable to suppose that an adaptive switch from despotic to ideal-free



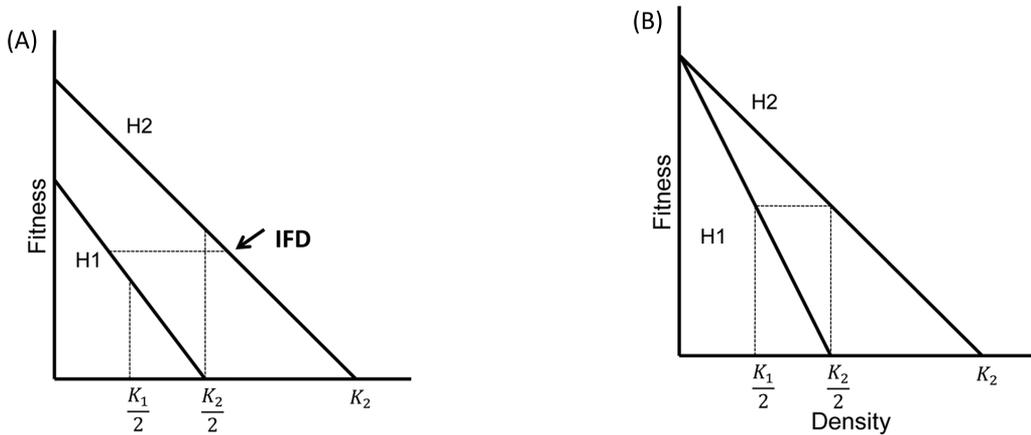


Fig. 7. An example illustrating that the buffering effect of ideal-free habitat selection depends on the relationships between fitness and density. In (A), an ideal-free distribution (IFD, horizontal dashed line) yields a lower population size in habitat 1 (H1), and a higher size in habitat 2 (H2), than population sizes that maximize population growth (vertical lines at $\frac{1}{2}K$). In (B), the ideal-free distribution maximizes population growth.

habitat selection at low densities might be a more likely mechanism to rescue populations from extinction than would be the evolution of extreme competitive dominance.

The results from our experiments with meadow voles are consistent with switching habitat-selection strategies. Voles given a choice between enclosures prior to supplemental feeding existed at similar densities and achieved similar foraging success (no difference in GUDs). Control populations restricted to single habitats in adjacent enclosures diverged in both density and GUDs. Giving-up densities were higher in enclosures with supplemental food, and dropped precipitously in enclosures without supplements, whether voles had an opportunity to disperse or not.

Regardless of differences in GUDs, our field experiments provide only a partial glimpse of how habitat selection might rescue populations from, or drive them to, extinction. Patterns in GUDs and net dispersal were consistent with a shift from IFD to IDD habitat selection, but not observations of movement between habitats, temporal differences in population density, or patterns of association with personality or condition. It is thus necessary to revisit each one in turn.

Giving-up densities, particularly in the no-supplement habitats, displayed a marked saw-tooth pattern. Mean GUDs were lower on day 1 than on day 2. We interpret this interesting result as a response to changes in energetic state. Foraging on day 1 followed four days when animals had no access to food in the trays, and during which their energetic state could decline. Foraging on day 2 followed only a single day without oats in the trays. Voles replenishing their state by eating oats one day prior to our day-2 GUDs may have been in a higher energetic state, and thus placed less value on food at this time, than did the same voles foraging on day 1. This interpretation is bolstered by the lower values of GUDs observed in enclosure E3 where voles were restricted to the poor habitat versus that in enclosure E4 where our photographs reveal substantial movement between that enclosure and its rich neighbour (E2).





The sawtooth pattern could arise from differences in energetic state only if consuming oats from trays represents a substantial energetic return to the population of rodents. Rodents restricted to a single enclosure could consume, at most, 64 g of oats during each foraging period (4 pairs of trays with 8 g each). Morris (2014) calculated that an average-sized adult vole requires approximately 7 g of whole oats a day to meet its energetic requirements. With maximum densities approaching 40 individuals of varying size (Fig. 5), and with GUDs approaching zero in enclosure E3 (Fig. 6), each foraging interval could thus provide in the neighbourhood of 20% of each animal's daily energetic needs. Our sawtooth data suggest that this rate of provisioning has a potential carryover onto subsequent foraging for at least 24 h.

Changes in energetic state should also influence foragers' assessments of predation risk (Brown, 1988; Brown and Kotler, 2004). Animals in a low energetic state should accept greater risk in order to secure food than individuals in a higher energetic state that have much lower prospects of starvation. Such an effect in our experiments would create a difference in GUDs between safe (cover) and risky (open) foraging trays. This pattern is one of the most striking of those revealed in our foraging data. Giving-up densities were higher under cover than in the open in all enclosures, but the mean difference was least in enclosure E3 where individuals had no opportunity to forage in the food-supplemented habitat.

It would nevertheless appear difficult to reconcile the dramatic differences in GUD, and the net flow of individuals between E2 and E4, with the absence of differences in population density, movement through gates, personality, and condition. Difficult as that may be, the similarities in personality, condition, and mean body size appear to rule out a truncated phenotype distribution (Milinski and Parker, 1991) for these populations of meadow voles. Even so, the difficulty in aligning our results with theory may be more apparent than real. If potential dispersers from poor habitat respect the property rights of those occupying (and born in) the rich one, then there is no reason to assume behavioural differences between the two groups of animals.

We can gain additional insights from simulations that assessed the success of despotic habitat choice where contests determined habitat occupation versus pre-emptive models of habitat selection in which individuals simply respected already established breeding sites (Morris and MacEachern, 2013). The simulations revealed a marked advantage for pre-emption, even with invasion by despotic individuals. Although the two strategies frequently co-existed in the simulations, the rank density of pre-emption was consistently higher than that for despotism.

One reason for pre-emption's superiority is that individuals pay only the cost of searching for an available site, rather than costs of acquiring and defending territory. Search costs in our field experiment would be accrued by all animals regardless of habitat quality, so one would not expect differences between enclosures in the personalities of pre-emptive habitat selectors. This does not necessarily mean that dispersers are a random subset of the population. Eight of nine dispersing voles were males that may have been searching more for mating opportunities (e.g. Greenwood, 1980; Gauffre *et al.*, 2009) than for resources.

Our personality assessments depart from the frequently reported bold versus shy continuum that typifies much of the personality literature (e.g. Luttbeg and Sih, 2010; Toms *et al.*, 2010) and are more in tune with the suggestion that 'activity' represents a separate category of temperament (Réale *et al.*, 2007). A forager's behaviour, and particularly its boldness in the face of danger, depends on the animal's state (Luttbeg and Sih, 2010). In this context, the low GUDs in enclosure E3, and the even lower difference in GUDs between open and covered





trays, reveal that voles living there were bolder than voles living elsewhere. Whatever our PC axes represent, they appear not to relate directly to foraging decisions or to have influenced habitat selection.

The bulk of evidence nevertheless supports a shift from ideal-free to despotic habitat selection and its inevitable Tragedy of the Commons. But our simulations also tell us that the tragedy need not end in collapse, and that the ability of either form of habitat selection to cause extinction, or rescue populations near the precipice of collapse, depends critically on habitat quality and environmental variability. Unfortunately, anthropogenic fragmentation of habitat and increasing climatic instability associated with global warming, do not augur well for the ability of these mechanisms to forestall the extinction of Earth's biodiversity.

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