An experimental test of Hamiltonian habitat selection

Kerman Bajina[1,2], Douglas W. Morris[1] and Per Lundberg[3]

*[1]Department of Biology, Lakehead University, Thunder Bay, Ontario, Canada,
[2]EDI Environmental Dynamics, Inc., Whitehorse, Yukon, Canada and [3]Theoretical Population
Ecology and Evolution Group (ThePEG), Department of Biology, Lund University, Lund, Sweden*

ABSTRACT

Question: Does a population of clones choose habitat according to inclusive or to individual fitness?

Theory: Gompertz equation, evolutionarily stable strategies, isodars, ideal free distribution.

Study species: *Folsomia candida* (Collembola).

Methods: We manipulated habitat quality by modifying moisture concentrations of substrate in petri dishes occupied by a single clone. We varied the abundance of animals, allowed them to lay a single clutch, and used the number of emergent adult offspring to estimate the effect of density on fitness. We used the fitness functions to predict the evolutionarily stable strategies of habitat selection for selfish versus cooperating individuals. We divided dishes into two discrete habitats and released variable numbers of animals at the boundary to evaluate whether they chose habitats consistent with selfish versus cooperative strategies. We transferred animals choosing each habitat into new dishes composed only of that habitat, allowed the animals to lay a single clutch, and used the number of emergent adults to estimate fitness accrued by habitat selection. We used habitat isodars to test the theory by regressing the density in moist versus drier habitats.

Results: The relationship between fitness and population density was highly convex-upward in all habitats. Maximum fitness was similar in habitats with 100%, 37.5%, and 25% moisture, but was much less in the driest (12.5%) habitat. Fitness declined more rapidly with density after habitat selection than in controls. Differences in convexity enabled habitat-selecting *Folsomia* clones to produce isodars that achieved higher mean fitness than predicted for selfish individuals.

Conclusions: Related individuals choose habitat consistent with expectations of their inclusive fitness. Habitat isodars, predicted from theory and built by experiment, reliably revealed the emergent adaptive patterns of distribution and abundance.

Keywords: density-dependence, ESS, *Folsomia candida*, ideal free distribution, inclusive fitness, spatial dynamics.

INTRODUCTION

Feedback between ecology and evolution on the one hand, and the conservation of biodiversity on the other, would seem to be a promising research target. We need a thorough understanding of mechanisms underlying the spatial dynamics of populations to comprehend fully this feedback

---

(Holt, 1987; Tregenza, 1995; Morris, 2003a; Morris and Lundberg, 2011). Spatial regulation occurs through the interaction between density-dependence within habitats (Rosenzweig, 1981) and dispersal among them (Holt, 1985; Morris, 1988; Rodenhouse *et al.*, 1997; Morris *et al.*, 2004; Moses *et al.*, 2013). If organisms are ideal habitat selectors, the habitat isodar – the set of densities among habitats that equalizes expected fitness (Morris, 1988) – uniquely reveals all alternative forms of spatial regulation. Isodars also help explore temporal regulation within source-sink systems (Morris, 2011a) and interactions among co-existing species (Morris, 1988, 2003b; Morris *et al.*, 2000). Quantitative and qualitative differences in habitat, which generate each habitat's relationship to fitness (Morris, 1988, 1989, 2011b), dictate the isodar, and thus the form of spatial regulation (Morris, 1988).

Optimal habitat selectors will disperse to match the pattern of their density with the pattern of likely habitat differences in fitness (Morris and Davidson, 2000). If unrelated individuals are unconstrained in their occupation of habitat, then they will obey an ideal free distribution (IFD) in which habitat selection equalizes mean fitness among habitats (Fretwell and Lucas, 1969). But evolutionary interests depend on the degree of relatedness (Hamilton, 1963; Gardner and Welch, 2011). So when individuals are related, it is reasonable to ask whether the apparently evolutionarily stable strategy (ESS) of the IFD will resist invasion from an alternative strategy (Morris *et al.*, 2001). The answer depends on the inclusive fitness achieved by altruistic individuals that sacrifice occupation of a good habitat in favour of a poor one [so-called MAXN habitat selection (Morris, 2011a)].

We answer the question with controlled experiments. We begin by briefly assessing IFD and MAXN strategies and evaluate how to differentiate between them. We then predict the expected outcomes of density-dependent habitat selection on populations of a parthenogenetic, clonal hexapod, *Folsomia candida* (a springtail). We describe how we estimated fitness in different habitats across a range of population sizes, and how we merged those estimates with replicated experiments to test the theory. We evaluate the fit between data, theory, and the life history of *F. candida*. We conclude by clarifying the role of genetic relatedness ('Hamiltonian' habitat selection) in creating spatial patterns in the distribution and abundance of organisms.

THEORY

Strategies and fitness of habitat selectors

Assessments of evolutionary strategies, including ideal free habitat selection, typically imagine an endpoint yielding one or more uninvadable strategies that coincide with long-term adaptation (e.g. Lehmann *et al.*, 2016). We thus expect that a population of entirely unrelated individuals with free choice between two alternative habitats should achieve an IFD through each selfish individual's decision to occupy the habitat that yields the higher fitness. The larger problem is to determine the appropriate forms of density-dependence (Travis *et al.*, 2013) and measures of fitness (e.g. Metz *et al.*, 1992), particularly in heterogeneous, stochastic, and time-varying environments (Melbinger and Vergassola, 2015; Sæther and Engen, 2015).

Behavioural decisions exacerbate the problem. The spatio-temporal variance in adaptive cues that individuals use to make decisions in the short term is unlikely to correspond to long-term adaptation tuned by demography and environment. Should those behavioural decisions reflect short-term (e.g. mean individual fitness reflecting the organism's perception of current conditions) or long-term (e.g. geometric mean fitness) adaptation? In short-term experiments, we may assume that individual fitness [the number of offspring produced in a short interval of time plus the likelihood of parental survival (Sæther and Engen, 2015)] should reflect both time-scales – adaptive decisions and long-term evolutionary adaptation. Although one may question the

validity of this assumption (Giraldeau and Dubois, 2008; Fawcett *et al.*, 2013), underlying psychological mechanisms should yield near-optimal behaviours in environments familiar to the organism (Fawcett *et al.*, 2013).

Related individuals should maximize inclusive, rather than selfish, fitness (Hamilton, 1964; Morris *et al.*, 2001). So an appropriate fitness metric in a population of multiple clones will measure changes in the frequency of clones, rather than changes in the frequency of traits or alleles. If the fitness of alternative clones is constant in time and space, the clone that achieves the largest population size will replace all others. Thus, when we deal with a single clone, such as those we establish with *Folsomia candida*, population growth and individual fitness converge. In essence, a clone is only one individual, albeit one composed of multiple organisms.

The model

Assume a population of identical organisms with discrete generations occupying two habitats that differ in quality. The model must evaluate and track the resources (per capita) allocated to reproduction and survival. If the allocation of those resources changes as population size grows, then the rate of fitness decline can decelerate with increasing population size. Competition for resources that is low at small population sizes is likely to intensify in large populations when interactions with many competing organisms increase the proportion of consumed resources allocated to competitive survival-enhancing activities. One effective way to capture these effects is to model fitness with a phenomenological version of a discrete-time Gompertz (1825) equation, such as that used by Dennis *et al.* (2006):

$$N_{i(t+1)} = N_{i(t)} e^{r_i - b_i \ln N_{i(t)}}, \tag{1}$$

where N is population size in habitat i at times t and $t + 1$, r is the intrinsic rate of population growth, and b is the strength of density-dependence. Converting equation (1) to natural logarithms and rearranging yields the convex-upward relationship:

$$\ln N_{i(t+1)} - \ln N_{i(t)} = r_i - b_i \ln N_{i(t)}. \tag{2}$$

If individual organisms select one of the two habitats in order to maximize their individual fitness and are free to occupy the habitat they select, then they will achieve an ideal free distribution [IFD (Fretwell and Lucas, 1969)]:

$$r_2 - b_2 \ln N_{2(t)} = r_1 - b_1 \ln N_{1(t)}. \tag{3}$$

Rearranging equation (3) to solve for N_2 provides the curvilinear ideal free habitat isodar in the space (N_1, N_2), i.e. the set of density pairs that equalize mean fitness (evolutionary-ecology.com/data/3216Appendix.pdf):

$$N_2 = \left[e^{\frac{r_2 - r_1}{b_2}} N_1^{\frac{b_1}{b_2}} \right]. \tag{4}$$

When individuals are unrelated, the ideal free isodar is an ESS (Cressman and Křivan, 2006), and moving to a different habitat is not adaptive for any individual. But such a strategy does not maximize per-capita population growth rate when individual organisms are related. Related organisms that maximize inclusive fitness through habitat selection should sacrifice individual fitness for the benefit of relatives [MAXN (Morris *et al.*, 2001; Morris, 2011a)]. Dispersal among habitats will cease for the MAXN strategy (Appendix A) when

$$N_2 = \left[e^{r_2}(1 - Rb_2) \right]^{\frac{1}{b_2}} \left[e^{r_1} N_1^{-b_1}(1 - Rb_1) \right]^{-\frac{1}{b_2}}, \tag{5}$$

where R is the coefficient of relatedness ($0 \leq R \leq 1$) of individuals, valued at 1 for clones (Morris *et al.*, 2001).

A particularly interesting solution to equation (5) emerges with high levels of genetic relatedness and density-dependence ($b_i \geq 1$). The isodar is undefined. Thus, as population size increases, individuals have no habitat to occupy and maximize inclusive fitness by self-sacrifice. In cannibalistic clonal species such as *F. candida*, a self-sacrificing individual provides nourishment to kin (itself) which can then be allocated towards future reproduction. The ancient Egyptians drew an iconograph – the *ouroboros*, i.e. a snake in a circle eating its own tail – to represent the behaviour of eating oneself. Aptly, it is a fertility symbol. It is unclear how frequent such an apparently paradoxical '*ouroboros* ESS' might be, but one cannot ignore the possibility of its existence.

Testing the model

We test whether the MAXN strategy yields higher population growth than does the IFD in clonal populations of *F. candida* given a choice between habitats of contrasting quality. We seek to answer three questions: (1) Does the Gompertz model reveal differences among habitats in the relationship between fitness and density? (2) Does habitat selection by *F. candida* fit the isodars expected by those relationships? And (3) do *F. candida* select habitat in a way that maximizes inclusive fitness (MAXN)?

We answer these questions with clones of *F. candida* descended from a single ancestor. We create high- to low-quality habitats by manipulating substrate moisture concentrations. Then we inoculate each habitat type with *F. candida* across a range of population sizes. We fit the relationship between fitness and density in each of these control habitats with the Gompertz model of population growth. We use those relationships to calculate the IFD and MAXN isodars expected for animals choosing between pairs of habitats that differ in quality. We also allow populations of different sizes to select between the two habitats, measure the fitness accrued by those choices, then contrast their actual distributions and fitnesses with those expected from the controls.

METHODS

Study populations

We used cloned populations of *Folsomia candida*, an exclusively female, parthenogenetic hexapod whose biology is well known because of its widespread use in eco-toxicological research (Pedersen *et al.*, 2000; Fountain and Hopkin, 2005). When the parasitic bacterium *Wolbachia* (Riparbelli *et al.*, 2006) infects the eggs, it induces automictic parthenogenesis (Stenberg and Saura, 2009). Terminal fusion during meiosis causes reproduction to be functionally mitotic (Ma and Schwander, 2017) with the potential to create clonal lineages (Tully *et al.*, 2006) favouring the evolution of altruistic strategies.

Folsomia candida reproduction depends on density. Crowding (> 1 animal/cm^2) reduces egg-laying (Green, 1964; Fountain and Hopkin, 2005).

Folsomia candida is also a density-dependent habitat selector, and individuals select habitat depending on their energetic state (Bannister and Morris, 2016). It can identify and disperse to moist

habitat when exposed to mixtures of moist versus dry substrate (Joosse and Groen, 1970; Verhoef and van Selm, 1983; Bannister and Morris, 2016). *Folsomia* stressed by desiccation initiate sugar and polyol production to help maintain water balance (Bayley and Holmstrup, 1999), which likely explains a stress-induced trade-off between survival and reproduction (Appendix B).

Individuals tend to aggregate through conspecific attraction (Verhoef *et al.*, 1977; Nilsson and Bengtsson, 2004) elicited by olfactory sensing of fatty acids stored in the animals' cuticles (Liu and Wu, 2017). But they show no evidence of social structure or social behaviour (Amorim *et al.*, 2005). Cannibalistic feeding on eggs (Fountain and Hopkin, 2005) and conspecifics (Negri, 2004) reduces individual fitness. Cannibalism is particularly interesting in our experiments because animals, and their eggs, are identically related. Individuals that consume eggs and conspecifics are – like the *ouroboros* iconograph – eating themselves.

Habitat selection and fitness

We synchronized the age of primiparous *F. candida* individuals in all cloned cultures and allowed them to grow under identical conditions. This eliminated maternal effects and ensured that all animals in control and treatment populations were in the same state. We removed these animals after all of them had the opportunity to lay a single clutch of eggs. Then we counted the number of descendants that reached adult size. *Folsomia candida* life span (which varies with temperature) ranges from about 100 to 200 days. During that time, adults produce clutches at approximately 10-day intervals (Fountain and Hopkin, 2005). So we assumed in our fitness calculations that the young egg-laying females in our experiments would have survived to reproduce in future if given the opportunity. We used controls to measure fitness of fixed densities of animals in each habitat. We measured fitness in habitat-selection treatments at the densities made by individuals choosing habitats.

We created controls by pouring substrate into single petri dishes. We enabled habitat selection in other dishes by pouring substrate into three interconnected compartments (Appendix B). Animals in the habitat-selection dishes could choose between two distinct habitats adjacent to a central release site. Animals in controls were restricted to the single habitat of their dish.

We used four substrate moisture concentrations to vary habitat quality (high quality = 100% water saturation; moderate quality = 37.5% water saturation; moderately low quality = 25% water saturation; and low quality = 12.5% water saturation) (Appendix B). We monitored habitat selection in 80 populations (20 from each of four age-synchronized cultures).

We allowed animals to disperse in the habitat-selection dishes, then photographed each dish 24 hours later. We displayed the photographs on a computer monitor, and counted the number of individuals in each habitat. We converted abundances to densities standardized to the area of whole petri dishes (58 cm^2) and used those values to generate habitat isodars. While habitat-selecting animals occupied compartmented dishes, animals living in control dishes (a total of 96 populations) experienced only a habitat of 100% moisture.

We transferred all populations into new petri dishes with their respective homogeneous habitats of 12.5%, 25%, 37.5%, and 100% moisture, as assigned by us (controls) or chosen by the animals (habitat selection). We placed a single yeast pellet in the centre of these new dishes. We kept animals in these dishes for a quiescent period in order to eliminate potential state-dependent carryover effects associated with our initial culture conditions (Wallenstein and Fisher, 1977; Norris, 2005; Harrison *et al.*, 2011; O'Connor *et al.*, 2014; Bannister and Morris, 2016). We then transferred each population to a new dish (again with a single yeast pellet) of the same habitat. We removed the adults after allowing them to lay eggs, thus simulating discrete generations so as to fit the

Gompertz model of population growth. We allowed eggs to hatch and mature while renewing moisture and the yeast pellet weekly. We photographed the newly recruited adults in each dish, displayed the images on a computer monitor, and counted the individuals plus their mothers; this became our measure of density in the subsequent generation.

Statistical analysis

Fitness and density

We linearized equation (2) and estimated maximum population growth (r_i) and density-dependence (b_i) with least-squares regression. To discount differences in sample size between control ($n = 24$) and habitat-selection populations ($n = 20$, except in the lowest quality habitat where extinction of a population with only 3 animals reduced the number of replicates to 19), we resampled 20 of the 24 control data points without replacement to create 10,000 'bootstrapped' regressions. We evaluated whether the intercepts and slopes from the analysis of the complete data fell within the 95% confidence interval of these estimates. Sample sizes were disproportionately larger in high-quality habitat ($n = 100$) because each habitat-selection petri dish included that habitat. Using a general linear model (GLM, Appendix C), we investigated whether mean fitness achieved in this high-quality habitat differed depending on treatment.

Habitat selection

We created empirical isodars by regressing density in high-quality (100% moisture) habitat against the respective density in each alternative habitat. We transformed all density values to natural logarithms in order to conform to the linearized Gompertz expectation (e.g. for the IFD):

$$\ln N_2 = \frac{r_2 - r_1}{b_2} + \frac{b_1}{b_2} \ln N_1. \tag{6}$$

We analysed each isodar with standard major axis regression (Morris, 1987; 'smatr' package in R software, Warton *et al.*, 2012; R Development Core Team, 2013).

We calculated IFD and MAXN isodars for each set of paired habitats from the corresponding control fitness functions using equations (4) and (5) respectively. We used the isodar solutions to predict the density of animals that should occupy high-quality habitat for every density that habitat selectors achieved in alternative habitats. These predictions often yielded partial individuals, so we rounded predictions to the nearest integer. As with empirical isodars, we transformed all density values to their natural logarithms and analysed each expected isodar with standard major axis regression.

We tested whether the isodars of habitat-selecting *F. candida* better corresponded with IFD (equation 4) or MAXN (equation 5) expectations. We complemented this analysis by using the fitness equations from the controls to calculate, for all population sizes, the per-capita population growth expected from every possible distribution of animals inhabiting each habitat. We then determined which combinations minimized the differences between habitats in per-capita population growth (which corresponds to an IFD), and which ones maximized total population growth (MAXN). The MAXN strategy requires that individuals in one habitat sacrifice their individual fitness for the benefit of kin occupying the alternative habitat. We searched for this effect by evaluating whether mean per-capita fitness following habitat selection was greater in one habitat than the other (paired *t*-test).

RESULTS

Fitness and density

All fitness functions were highly convex-upward with long flat tails that yielded similar fitness at high densities (Fig. 1). Fitness, and its relationship with density, differed among habitats and between control and habitat-selection experiments (Fig. 1). We attribute this pattern to the joint effects of habitat selection and habitat quality. Although our treatments used the same population sizes, the number occupying lower-quality habitat after habitat selection was less than in the control without habitat selection. The result was different relationships of fitness and density between controls and habitat-selection treatments, and dramatic differences among habitats within treatments (Fig. 1). The number of individuals occupying the 100% habitat following habitat selection was much greater than in habitats of lower quality (25% and 37.5% moisture).

When quality was even lower (12.5% moisture), maximum fitness of habitat-selecting *F. candida* was less than in any other habitat. The low maximum reduced the mean fitness to that of the long-tailed 100% habitat dishes. But this was inconsistent with control experiments, where fitness in the saturated (100%) habitat was higher at all densities than in the low-quality (12.5%) habitat (Fig. 1).

Habitat selection

All isodar regressions were highly significant and confirmed the expectation that more individuals should occupy high- than low-quality habitat (Fig. 2). Empirical and expected isodars were similar in dishes composed of identical 100% moisture habitats, as well as in dishes enabling selection between high- (100%) and moderately-low-quality (25%) habitats and high- (100%) and low-quality (12.5%) habitats (Fig. 2, Table 1). The empirical isodar intercept was higher than IFD and MAXN predictions, and the slope lower, in dishes allowing habitat selection between high-quality and moderate-quality (37.5%) habitats. We were concerned that the apparently atypical data from the lowest density in the 37.5% treatment (Fig. 2) caused the significant departure from expectation. We repeated the isodar analysis after removing that data-point. The removal decreased the intercept (1.29 vs. 1.68) and increased the slope (0.79 vs. 0.73) while also reducing the fit of the model ($R^2 = 0.78$ vs. 0.86). The conclusion was the same. The intercepts and slopes of the IFD and MAXN predictions were outside of the 95% confidence limits of the data-reduced isodar. Although differences were subtle, empirical isodars, on the whole, tended to be more similar to expectations of the MAXN distribution than to those of the IFD (Table 1, Fig. 2).

Comparisons of all possible distributions of individuals among habitat pairs revealed an intriguing difference between IFD and MAXN solutions. All IFD solutions yielded a single best strategy of one pair of densities at each population size (Fig. 3). But the MAXN solutions yielded an increasingly wide range of density pairs that produced identical maximum population sizes in the next generation. A clear example is the MAXN solution contrasting high- versus moderately-low-quality habitats (100% vs. 25% moisture, Fig. 3). The existence of multiple 'strategies' yielding identical outcomes is intriguing because it demonstrates the potential of multiple isodars that can diverge from one another, or meander among equal-fitness alternative densities at different population sizes (Fig. 3). The cloud of possible isodars should nevertheless cluster around the theoretical isodar (MAXN) predicted from equation (5).

Mean per-capita fitness was not different from zero (IFD) when animals chose between habitats of equal quality (100%), or when they chose between extreme habitats (100% vs.
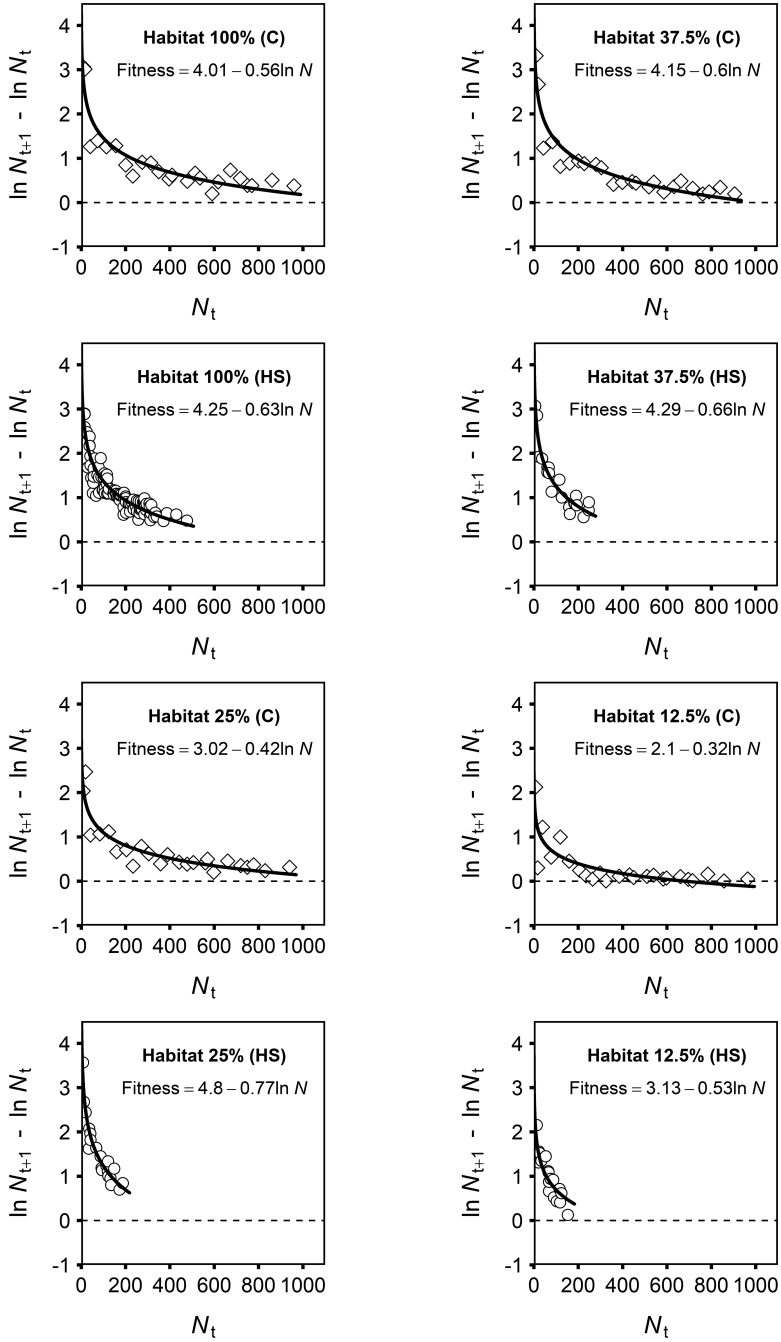
Fig. 1. Relationships between fitness (equation 2) and density (N_t) in each of four habitats (12.5%, 25%, 37.5%, and 100% moisture) occupied by *Folsomia candida* in control (C, diamonds) and habitat selection (HS, circles) experiments.

Table 1. Empirical and expected IFD and MAXN habitat isodars of clonal *Folsomia candida* choosing between habitats varying in moisture concentration. Empirical regressions fit closely with MAXN expectations in all but one habitat comparison (100% vs. 37.5%)

Habitat comparison (% moisture)	Empirical isodars				Expected isodars			
					IFD		MAXN	
	Intercept	Slope	R^2	P	Intercept	Slope	Intercept	Slope
100 vs. 100 ($n = 20$)	−0.22 L (−1.08) U (0.64)	1.00 L (0.86) U (1.15)	0.91	< 0.001	0 (0)	1 (1)	0 (0)	1 (1)
100 vs. 37.5 ($n = 20$)	1.68 L (0.89) U (2.47)	0.73 L (0.60) U (0.88)	0.86	< 0.001	**−0.25** (−0.21)	**1.07** (1.06)	**−0.08** (−0.02)	**1.07** (1.06)
100 vs. 25 ($n = 20$)	1.06 L (0.12) U (2.00)	0.91 L (0.75) U (1.09)	0.85	< 0.001	1.77 (1.65)	0.75 (0.76)	1.27 (1.07)	0.75 (0.76)
100 vs. 12.5 ($n = 20$)	2.46 L (1.61) U (3.31)	0.72 L (0.57) U (0.91)	0.78	< 0.001	**3.41** (3.05)	0.57 (0.61)	2.63 (2.18)	0.57 (0.61)

Note: All isodars based on standard major axis regressions of logarithmically (ln N_t) transformed density. Lower (L) and upper (U) 95% confidence intervals provided for empirical isodars in order to detect significant differences (**bold** font) from expected values; parenthetical values are parameter estimates obtained from rarefied densities.

12.5%). Mean fitness was higher, however, in the 37.5% and 25% habitats than in their respective high-quality alternative choices (Table 2). This pattern did not depend on population size (GLM, $F_{1,35} = 0.64$, $P = 0.4$) and led to lower than expected population growth of habitat-selecting *F. candida* choosing between high- versus moderate-quality (100% vs 37.5%) habitats.

DISCUSSION

Habitat selection depends on density

Interpretations of our results must first discount the null hypothesis that habitat occupation by *F. candida* occurred by chance, rather than through active choice. We released animals along the boundary between habitats. There are two possible 'random' outcomes. First, animals might use conspecific attraction to aggregate on one side or the other independent of density; the isodar regression would not be statistically significant. The highly significant isodar regressions reject this hypothesis.

Second, animals moving at random might occupy both habitats equally; the isodar would pass through the origin with slope = 1. The null hypothesis is consistent with the control isodar comparing habitats of equal quality (100 vs. 100; Table 1), but so too is active habitat selection. But the remaining three isodars comparing habitats of unequal quality reject random movement. None of the confidence limits includes an intercept of zero, and only one isodar (100 vs. 25) has a slope not different from unity. *Folsomia candida* is a density-dependent habitat selector.
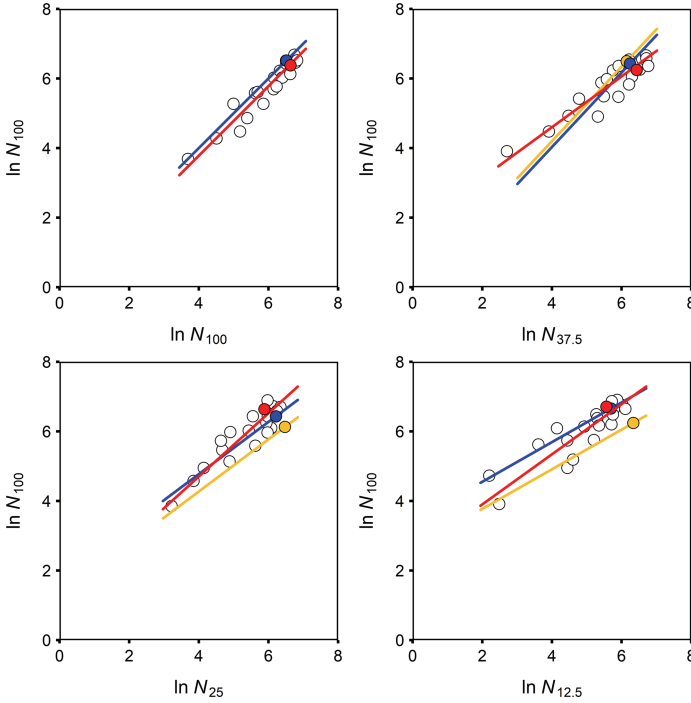
Fig. 2. Empirical (red, open circles) and expected IFD (blue) and MAXN (gold) isodars of *Folsomia candida* populations occupying petri dishes with four different pairs of habitats varying in moisture concentration. Red-, blue-, and gold-filled circles represent the values of empirical, IFD, and MAXN isodar solutions obtained at the same total population size (100% vs. 100%, $N = 1351$; 100% vs. 37.5%, $N = 1139$; 100% vs. 25%, $N = 1121$; 100% vs. 12.5%, $N = 1080$). IFD and MAXN expectations are identical in the comparison between the two 100% habitats. All empirical isodars based on standard major axis regressions of logarithmically transformed density (ln N_t).
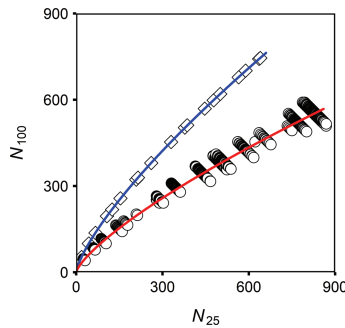
Fig. 3. Expected IFD and MAXN isodars (linear scale) for *Folsomia candida* choosing between high- versus moderately-low-quality (100% vs. 25%) habitats. IFD (diamonds) and MAXN (circles) isodar solutions based on all possible comparisons of density (N) at 20 different population sizes. Blue and red lines correspond with solutions (from Fig. 1) to equations (4, IFD) and (5, MAXN) respectively.

Table 2. Summary of two-tailed paired *t*-tests assessing fitness differences between pairs of habitats chosen by *Folsomia candida*. Significant negative values correspond to higher fitness in 'low-quality' habitat

Habitat comparison (% moisture)	Mean difference	Fitness differences 95% CIs		t	P
		Lower	Upper		
100 vs. 100 ($n = 20$)	−0.06	−0.14	0.03	−1.44	0.2
100 vs. 37.5 ($n = 20$)	−0.22	−0.37	−0.08	−3.20	0.005
100 vs. 25 ($n = 20$)	−0.40	−0.57	−0.23	−4.90	< 0.001
100 vs. 12.5 ($n = 20$)	−0.11	−0.28	0.06	−1.38	0.2

Folsomia candida maximized inclusive fitness

Habitat selection by clonal populations of *F. candida* was more consistent with a strategy based on inclusive fitness (MAXN) than it was with one maximizing individual fitness (IFD). This result is especially intriguing because *F. candida* appears to have no social structure or social behaviour (Amorim *et al.*, 2005) capable of creating cooperative choices consistent with Hamiltonian habitat selection. Even so, closely related individuals chose between habitats in a manner consistent with the sacrifice of individual fitness for the benefit of kin. One possibility is that close-kinship associated with parthenogenetic reproduction pre-programmes individuals with behaviours that maximize inclusive rather than individual fitness.

Other potential causes of habitat choice by *F. candida* are no less intriguing. *Folsomia candida* are attracted to conspecific fatty acids (Liu and Wu, 2017). The attraction is likely to represent a form of public information (Valone, 1989; Danchin *et al.*, 2004) that the animals can use as an indirect cue of habitat quality. If that cue also depends on density, then it might help to explain why both density and fitness vary with habitat choice. The same would be true of any mechanism causing animals to avoid one or the other habitat, such as predator evasion (Santonja *et al.*, 2018) or conspecific repulsion (Nilsson and Bengtsson, 2004; Liu and Wu, 2017).

Whatever the cause, habitat selection by *F. candida* depends on highly convex-upward fitness functions that are likely caused by habitat-selecting relatives maximizing their inclusive fitness through suicidal egg cannibalism. Although increased maternal survival through egg cannibalism can yield convex-upward relationships of fitness with density, it is also possible to produce more recruits if relaxed competition among hatchlings enhances juvenile survival [e.g. via 'supersoft selection' (Agrawal, 2010)]. We nevertheless wonder whether other forms of kin behaviour can account for the convex-upward relationships between population growth rate and density that appear prevalent across major taxonomic groups of animals (Sibly *et al.*, 2005).

Strong tests of habitat selection merge theory with experiment

Our tests of habitat selection by *F. candida* highlight the value of testing theory with experiments that yield *a priori* predictions of habitat preference. The relationship between fitness and density

varied among habitats with different substrate moisture concentrations. The long and flattened tails of each distribution document a deterioration in the effect of density-dependence on fitness at large population sizes. We used those relationships to determine the optimal habitat occupation predicted by two divergent models of habitat selection. Paradoxically, when mean per-capita fitness differed between habitats, it was higher in low-quality habitat than in high-quality habitat. Our data explain why. Fitness curves generated from habitat selection were less convex-upward than were those of control populations growing in a single habitat. Heightened competition associated with density-dependent habitat selection compressed all fitness curves towards lower densities. The compression was most intense in low-quality habitats. Mean fitness was thereby inflated in those habitats because fewer individuals occupied the tail of the fitness distribution.

Habitat selection was most obvious in the choice between 100% and 25% moisture substrates. The contracted tail of the 25% fitness function yielded a less convex-upward relationship than in controls, and thus enabled higher mean fitness than predicted. The tail contraction was less in the 37.5% dishes, the habitat-selection and control relationships were more similar, and so too was fitness.

If the tail of the distribution is so important to mean fitness, why then was mean fitness not greater than predicted in the most extreme comparison of selection between 100% versus 12.5% habitats? The answer lies not in the tail, but in the intercept. Animals choosing the 12.5% habitat achieved a much lower maximum fitness than did animals in all other habitats. The negative influence on the mean associated with low maximum fitness neutralized the otherwise positive effect of a shortened tail and less convex-upward function.

Our experiments demonstrate that genetic relatedness alone is insufficient to explain cooperative strategies of habitat selection. The impact of genetic relatedness on strategies of habitat selection depends on the shapes of the fitness curves. If one is to test the theory, then it is crucial to identify not only kin structure but also the influence of density-dependent habitat selection on fitness. Although those experiments are necessary to test theory, they are superfluous to their emergent isodars that reliably reveal adaptive patterns of distribution and abundance.

ACKNOWLEDGEMENTS

REFERENCES

Agrawal, A.F. 2010. Ecological determinants of mutation load and inbreeding depression in subdivided populations. *Am. Nat.*, **176**: 111–122 [https://doi.org/10.1086/653672].

Amorim, M.J.B., Römbke, J., Scheffczyk, A., Nogueira, A.J.A. and Soares, A.M.V.M. 2005. Effects of different soil types on the collembolans *Folsomia candida* and *Hypogastrura assimilis* using the herbicide Phenmedipham. *Arch. Environ. Contam. Toxicol.*, **49**: 343–352 [https://doi.org/10.1007/s00244-004-0220-z].

Bannister, A.E. and Morris, D.W. 2016. Habitat selection reveals state-dependent foraging trade-offs in a temporally autocorrelated environment. *Isr. J. Ecol. Evol.*, **62**: 162–170 [https://doi.org/10.1080/15659801.2015.1065680].

Bayley, M. and Holmstrup, M. 1999. Water vapour absorption in arthropods by accumulation of myoinositol and glucose. *Science*, **285**: 1909–1911 [https://doi.org/10.1126/science.285.5435.1909].

Cressman, R. and Křivan, V. 2006. Migration dynamics for the ideal free distribution. *Am. Nat.*, **168**: 384–397 [https://doi.org/10.1086/506970].

Danchin, E., Giraldeau, L.-A., Valone, T.J. and Wagner, R.H. 2004. Public information: from nosy neighbors to cultural evolution. *Science*, **305**: 487–491 [https://doi.org/10.1126/science.1098254].

Dennis, B., Ponciano, J.M., Lele, S.R., Taper, M.L. and Staples, D.F. 2006. Estimating density dependence, process noise, and observation error. *Ecol. Monogr.*, **76**: 323–341 [https://doi.org/10.1890/0012-9615(2006)76[323:EDDPNA]2.0.CO;2].

Fawcett, T.W., Hamblin, S. and Giraldeau, L.-A. 2013. Exposing the behavioral gambit: the evolution of learning and decision rules. *Behav. Ecol.*, **24**: 2–11 [https://doi.org/10.1093/beheco/ars085].

Fountain, M.T. and Hopkin, S.P. 2005. *Folsomia candida* (Collembola): a 'standard' soil arthropod. *Annu. Rev. Entomol.*, **50**: 201–222 [https://doi.org/10.1146/annurev.ento.50.071803.130331].

Fretwell, S.D. and Lucas, H.L. 1969. On territorial behaviour and other factors influencing habitat distribution in birds. *Acta Biotheor.*, **19**: 45–52 [https://doi.org/10.1007/BF01601955].

Gardner, A. and Welch, J.J. 2011. A formal theory of the selfish gene. *J. Evol. Biol.*, **24**: 1801–1813 [https://doi.org/10.1111/j.1420-9101.2011.02310.x].

Giraldeau, L.-A. and Dubois, F. 2008. Social foraging and the study of exploitative behavior. *Adv. Study Behav.*, **38**: 59–104 [https://doi.org/10.1016/S0065-3454(08)00002-8].

Gompertz, B. 1825. On the nature of the function expressive of the law of human mortality, and on a new mode of determining the value of life contingencies. *Phil. Trans. R. Soc. Lond. B: Biol. Sci.*, **115**: 513–585 [https://doi.org/10.1098/rstl.1825.0026].

Green, C.D. 1964. The effect of crowding upon the fecundity of *Folsomia candida* (William) var. *distincta* (Bagnall) (Collembola). *Entomol. Exp. Appl.*, **7**: 62–70 [https://doi.org/10.1111/j.1570-7458.1964.tb00726.x].

Hamilton, W.D. 1963. The evolution of altruistic behaviour. *Am. Nat.*, **97**: 354–356 [https://doi.org/10.1086/497114].

Hamilton, W.D. 1964. The genetical evolution of social behaviour I. *J. Theor. Biol.*, **7**: 1–16 [https://doi.org/10.1016/0022-5193(64)90038-4].

Harrison, X.A., Blount, J.D., Inger, R., Norris, D.R. and Bearhop, S. 2011. Carry-over effects as drivers of fitness differences in animals. *J. Anim. Ecol.*, **80**: 4–18 [https://doi.org/10.1111/j.1365-2656.2010.01740.x].

Holt, R.D. 1985. Population dynamics in two-patch environments: some anomalous consequences of an optimal habitat distribution. *Theor. Popul. Biol.*, **28**: 181–208 [https://doi.org/10.1016/0040-5809(85)90027-9].

Holt, R.D. 1987. Population dynamics and evolutionary processes: the manifold roles of habitat selection. *Evol. Ecol.*, **1**: 331–347 [https://doi.org/10.1007/BF02071557].

Joosse, E.N.G. and Groen, J.B. 1970. Relationship between saturation deficit and the survival and locomotory activity of surface dwelling Collembola. *Entomol. Exp. Appl.*, **13**: 229–235 [https://doi.org/10.1111/j.1570-7458.1970.tb00106.x].

Lehmann, L., Mullon, C., Akçay, E. and Van Cleve, J. 2016. Invasion fitness, inclusive fitness, and reproductive numbers in heterogeneous populations. *Evolution*, **70**: 1689–1702 [https://doi.org/10.1111/evo.12980].

Liu, J. and Wu, D. 2017. Chemical attraction of conspecifics in *Folsomia candida* (Collembola). *J. Insect Behav.*, **30**: 331–341 [https://doi.org/10.1007/s10905-017-9620-6].

Ma, W.J. and Schwander, T. 2017. Patterns and mechanisms in instances of endosymbiont-induced parthenogenesis. *J. Evol. Biol.*, **30**: 868–888 [https://doi.org/10.1111/jeb.13069].

Melbinger, A. and Vergassola, M. 2015. The impact of environmental fluctuations on evolutionary fitness functions. *Sci. Rep.*, **5**: 15211 [https://doi.org/10.1038/srep15211].

Metz, J.A.J., Nisbet, R.M. and Geritz, S.A.H. 1992. How should we define 'fitness' for general ecological scenarios? *Trends Ecol. Evol.*, **7**: 198–202 [https://doi.org/10.1016/0169-5347(92)90073-K].

Morris, D.W. 1987. Tests of density-dependent habitat selection in a patchy environment. *Ecol. Monogr.*, **57**: 269–281 [https://doi.org/10.2307/2937087].

Morris, D.W. 1988. Habitat-dependent population regulation and community structure. *Evol. Ecol.*, **2**: 253–269 [https://doi.org/10.1007/BF02214286].

Morris, D.W. 1989. Density-dependent habitat selection: testing the theory with fitness data. *Evol. Ecol.*, **3**: 80–94 [https://doi.org/10.1007/BF02147934].

Morris, D.W. 2003a. Toward an ecological synthesis: a case for habitat selection. *Oecologia*, **136**: 1–13 [https://doi.org/10.1007/s00442-003-1241-4].

Morris, D.W. 2003b. Shadows of predation: habitat-selecting consumers eclipse competition between coexisting prey. *Evol. Ecol.*, **17**: 393–422 [https://doi.org/10.1023/A:1027304601301].

Morris, D.W. 2011a. Source-sink dynamics emerging from unstable ideal free habitat selection. In *Sources, Sinks and Sustainability* (J. Liu, V. Hull, A.T. Morzillo and J.A. Wiens, eds.), pp. 58–81. Cambridge: Cambridge University Press.

Morris, D.W. 2011b. Adaptation and habitat selection in the eco-evolutionary process. *Proc. R. Soc. Lond. B: Biol. Sci.*, **278**: 2401–2411 [https://doi.org/10.1098/rspb.2011.0604].

Morris, D.W. and Davidson, D.L. 2000. Optimally foraging mice match patch use with habitat differences in fitness. *Ecology*, **81**: 2061–2066 [https://doi.org/10.1890/0012-9658(2000)081[2061:OFMMPU]2 .0.CO;2].

Morris, D.W. and Lundberg, P. 2011. *Pillars of Evolution: Fundamental Principles of the Eco-evolutionary Process*. Oxford: Oxford University Press.

Morris, D.W., Davidson, D.L. and Krebs, C.J. 2000. Measuring the ghost of competition: insights from density-dependent habitat selection on the co-existence and dynamics of lemmings. *Evol. Ecol. Res.*, **2**: 41–67 [https://www.evolutionary-ecology.com/abstracts/v02/1047.html].

Morris, D.W., Lundberg, P. and Ripa, J. 2001. Hamilton's rule confronts ideal free habitat selection. *Proc. R. Soc. Lond. B: Biol. Sci.*, **268**: 921–924 [https://doi.org/10.1098/rspb.2001.1597].

Morris, D.W., Diffendorfer, J.E. and Lundberg, P. 2004. Dispersal among habitats varying in fitness: reciprocating migration through ideal habitat selection. *Oikos*, **107**: 559–575 [https://doi. org/10.1111/j.0030-1299.2004.12894.x].

Moses, M.M., Morris, D.W. and Qin, W. 2013. Greener on the other side of the fence: density-dependent habitat selection by a unicellular alga. *Evol. Ecol. Res.*, **15**: 809–828 [https://www.evolutionary-ecology.com/abstracts/v15/2869.html].

Negri, I. 2004. Spatial distribution of Collembola in presence and absence of a predator. *Pedobiologia*, **48**: 585–588 [https://doi.org/101016/j.pedobi.2004.07.004].

Nilsson, E. and Bengtsson, G. 2004. Endogenous free fatty acids repel and attract Collembola. *J. Chem. Ecol.*, **30**: 1431–1443 [https://doi.org/10.1023/B:JOEC.0000037749.75695.c5].

Norris, D.R. 2005. Carry-over effects and habitat quality in migratory populations. *Oikos*, **109**: 178–186 [https://doi.org/10.1111/j.0030-1299.2005.13671.x].

O'Connor, C.M., Norris, D.R., Crossin, G.T. and Cooke, S.J. 2014. Biological carryover effects: linking common concepts and mechanisms in ecology and evolution. *Ecosphere*, **5**: 1–11 [https://doi. org/10.1890/ES13-00388.1].

Pedersen, M.B., van Gestel, C.A.M. and Elmegaard, N. 2000. Effects of copper on reproduction of two Collembola species exposed through soil, food, and water. *Environ. Toxicol. Chem.*, **19**: 2579–2588 [https://doi.org/10.1002/etc.5620191026].

R Development Core Team. 2013. *R: A Language and Environment for Statistical Computing*. Vienna, Austria: R Foundation for Statistical Computing [http://www.R-project.org/].

Riparbelli, M.G., Giordano, R. and Callaini, G. 2006. Centrosome inheritance in the parthenogenetic egg of the collembolan *Folsomia candida*. *Cell Tissue Res.*, **326**: 861–872 [https://doi.org/10.1007/ s00441-006-0253-x].

Rodenhouse, N.L., Sherry, T.W. and Holmes, R.T. 1997. Site-dependent regulation of population size: a new synthesis. *Ecology*, **2**: 2025–2042 [https://doi.org/10.1890/0012-9658(1997)078[2025:SDROPS]2.0.CO;2].

Rosenzweig, M.L. 1981. A theory of habitat selection. *Ecology*, **62**: 327–335 [https://doi.org/10.2307/ 1936707].

Sæther, B.-E. and Engen, S. 2015. The concept of fitness in fluctuating environments. *Trends Ecol. Evol.*, **30**: 273–281 [https://doi.org/10.1016/j.tree.2015.03.007].

Santonja, M., Aupic-Samain, A., Forey, E. and Chauvat, M. 2018. Increasing temperature and decreasing specific leaf area amplify centipede predation impact on Collembola. *Eur. J. Soil Biol.*, **89**: 9–13 [https://doi.org/10.1016/j.ejsobi.2018.08.002].

Sibly, R.M., Barker, D., Denham, M.C., Hone, J. and Pagel, M. 2005. On the regulation of populations of mammals, birds, fish, and insects. *Science*, **309**: 607–610 [https://doi.org/10.1126/science.1110760].

Stenberg, P. and Saura, A. 2009. Cytology of asexual animals. In *Lost Sex: The Evolutionary Biology of Parthenogenesis* (I. Schon, K. Martens and P. van Dijk, eds.), pp. 63–74. Dordrecht: Springer.

Travis, J., Leips, J. and Rodd, F.H. 2013. Evolution in population parameters: density-dependent selection or density-dependent fitness? *Am. Nat.*, **181**: S9–S20 [https://doi.org/10.1086/669970].

Tregenza, T. 1995. Building on the ideal free distribution. *Adv. Ecol. Res.*, **26**: 253–302 [https://doi.org/10.1016/S0065-2504(08)60067-7].

Tully, T., D'Haese, C.A., Richard, M. and Ferrière, R. 2006. Two major evolutionary lineages revealed by molecular phylogeny in the parthenogenetic Collembola species *Folsomia candida*. *Pedobiologia*, **50**: 95–104 [https://doi.org/10.1016/j.pedobi.2005.11.003].

Valone, T.J. 1989. Group foraging, public information, and patch estimation. *Oikos*, **56**: 357–363 [https://doi.org/10.2307/3565621].

Verhoef, H.A. and van Selm, A.J. 1983. Distribution and population dynamics of Collembola in relation to soil moisture. *Holarctic Ecol.*, **6**: 387–394 [https://doi.org/10.1111/j.1600-0587.1983.tb01234.x].

Verhoef, H.A., Nagelkerke, C.J. and Joosse, E.N.G. 1977. Aggregation pheromones in Collembola. *J. Insect Physiol.*, **23**: 1009–1013 [https://doi.org/10.1016/0022-1910(77)90128-7].

Wallenstein, S. and Fisher, A.C. 1977. The analysis of the two-period repeated measurements crossover design with application to clinical trials. *Biometrics*, **33**: 261–269 [https://doi.org/10.2307/2529321].

Warton, D.I., Duursma, R.A., Falster, D.S. and Taskinen, S. 2012. SMATR 3 – an R package for estimation and inference about allometric lines. *Meth. Ecol. Evol.*, **3**: 257–259 [https://doi.org/10.1111/j.2041-210X.2011.00153.x].