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To cite this article: Allison E. Bannister & Douglas W. Morris (2016): Habitat selection reveals state-dependent foraging trade-offs in a temporally autocorrelated environment, Israel Journal of Ecology & Evolution, DOI: [10.1080/15659801.2015.1065680](https://doi.org/10.1080/15659801.2015.1065680)

To link to this article: <http://dx.doi.org/10.1080/15659801.2015.1065680>

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## Habitat selection reveals state-dependent foraging trade-offs in a temporally autocorrelated environment

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(Received 14 January 2015; accepted 20 June 2015)

We use theories of risk allocation to inform trade-offs between foraging in a rich and risky habitat versus using a poor but safe alternative. Recent advances in the theory predict that the length of exposure to good or bad conditions governs risk allocation, and thus habitat choice, when patterns of environmental risk are autocorrelated in time. We investigate the effects of these factors with controlled experiments on a small soil arthropod (*Folsomia candida*). We subjected animals to nine temporally autocorrelated 16-day feeding treatments varying in both the proportion (0.25, 0.50, and 0.75) and duration (short, medium and long intervals) of time when food was present and absent. We assessed foraging trade-offs by the animals' choice of occupying a risky dry habitat with food (rich) versus a safe moist habitat with no food (poor). Irrespective of autocorrelation in conditions, the proportion of time spent with no food primarily determined habitat selection by these collembolans. Our results imply an energetic threshold below which *F. candida* are forced to forage in rich and risky habitat despite the possibility of mortality through desiccation. The link to energetic thresholds suggests the possibility of employing state-dependent habitat selection as a leading indicator of habitat change.

**Keywords:** adaptive behaviour; energetic state; *Folsomia candida*; habitat selection; optimal foraging; risk allocation

### Introduction

Foraging theory recognizes that the decisions individuals make while foraging impact their evolutionary fitness. Choices of where and when to forage can determine whether or not an individual succumbs to predation or starvation. Foragers adopting an optimal foraging strategy should thus be selective and bias foraging efforts towards resource patches with the most favourable ratio of food availability to risk (Brown 1988; Brown et al. 1999; Kotler et al. 2010). Such individuals should reduce their feeding effort when predation risk is high and also increase anti-predator behaviours such as vigilance (Lima and Bednekoff 1999; Kotler et al. 2010). Conversely, individuals should increase feeding effort when the environment becomes less dangerous (Lima & Bednekoff 1999). These insights into the effects of predation on forager behaviour are described by the predation risk-allocation hypothesis (Lima & Bednekoff 1999) in which the trade-off between vigilance and foraging effort, and its interactions with a forager's energetic state, force hungry animals to accept more risk whenever predators become more active or abundant. Risk allocation thus represents a set of decisions that influence patch and space use by both predator and prey species (Embar et al. 2014). A clear understanding of foraging under regular risk regimes allows us to better comprehend the effects of predation on foraging behaviour, patch use, and habitat selection in temporally fluctuating environments (Sih et al. 2000).

Although tests of the risk-allocation hypothesis have yielded mixed results (Sih & McCarthy 2002; Koivisto &

Pusenius 2003; Sundell et al. 2004; Ferrari et al. 2009), it nevertheless predicts how foragers should trade-off food for safety. Most research, including recent theory that includes autocorrelated environmental conditions (Higginson et al. 2012), is directed towards assessing how foragers allocate risk through time. We suggest that those same theories can also inform decisions on the selection of safe versus risky habitats. We thus describe experiments that measured the use of a safe and resource poor habitat versus the use of a risky and resource rich habitat by populations of a small arthropod (the springtail *Folsomia candida*). In concert with a recent theory, we varied the foragers' energetic states by exposing them to different autocorrelated patterns of environmental change. In particular, we manipulated the proportion of time ( $p$ ) that animals were exposed to unfavourable conditions, the duration of those bad conditions ( $d$ ), and the length of time when animals were provisioned with food ( $f$ ).

We begin by briefly reviewing risk-allocation theory as it applies to habitat selection. We outline how we manipulated energetic state, and how we confirmed changes in energetic state by measuring survival and fecundity. We demonstrate how desiccation stress in Collembola serves as a general risk factor (Edney 1977; Fountain & Hopkin 2001; Bednekoff & Lima 2011). We describe the results and discuss their significance to our understanding of foraging trade-offs and risk-allocation behaviour. We conclude by discussing whether such behaviours enable us to detect changes in habitat before those changes cause populations to decline.

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### Predicting and testing risk-allocation behaviour

The original predation risk-allocation hypothesis (Lima & Bednekoff 1999) models the foraging behaviour of an individual over a specific time interval ( $T$ ) in which it must attain an energetic threshold ( $E$ ) in order to avoid starvation (Lima & Bednekoff 1999; Ferrari et al. 2009). Foragers in this model must allocate foraging between risky and safe periods according to their current energetic state and estimate of future environmental conditions. The theory predicts if periods of high risk are short or infrequent that optimal foragers should abstain from foraging during these brief pulses, reserving their foraging effort for better future conditions. As the proportion of time spent in risky conditions ( $p$ ) increases, the ability to reduce risk through vigilance or space use decreases during both safe and risky periods, as opportunities to forage in safety become rare, and the energetic state of foragers declines (Lima & Bednekoff 1999).

The decision to forage during risky times depends on whether the organism's current energetic state is sufficient to sustain the individual until safe times reappear (Higginson et al. 2012). In environments with no temporal autocorrelation, only the frequency of risky periods provides information on the probability of encountering safety. When the environment fluctuates predictably, however, organisms conditioned (e.g., cognitively or physiologically) to those fluctuations obtain more accurate predictions about the future environmental state from the duration of events ( $d$ ), than from  $p$ . Therefore, when safe and risky times fluctuate rapidly, animals should forage only during the safe periods. However, when safe and risky times fluctuate more slowly (longer durations of each event, and particularly so for risky periods), then less risk allocation (e.g., less vigilance and more foraging during risky periods) will increase survival. Similar interpretations hold when the forager's state depends on food-rich and food-poor intervals of time (Higginson et al. 2012).

When environments vary between periods of rich versus poor food abundance, the forager's optimal vigilance reflects its current energetic state, as well as its prior expectations on how its state varies through time. The interactions between energetic state and state-dependent and time-dependent vigilance should influence habitat selection. In order to appreciate their effects, imagine an experiment that exposes foragers to environments with differing periods and temporal patterns of food abundance and scarcity. After enduring such periods, the foragers are given a choice to occupy either a risky and rich habitat or a poor and safe one.

We illustrate these autocorrelated effects on the expected energetic states of hypothetical foragers in Figure 1 ( $p = 0.25$  in panels A and B;  $p = 0.5$  in panels C and D). In panels A and B, periods of resource scarcity are infrequent and foragers can regain their maximum energetic state by allocating high foraging vigilance that yields a relatively low energetic recovery rate during rich periods. In panels C and D, periods of both conditions are more frequent and foragers allocating the same level of vigilance cannot regain their energetic state. Longer

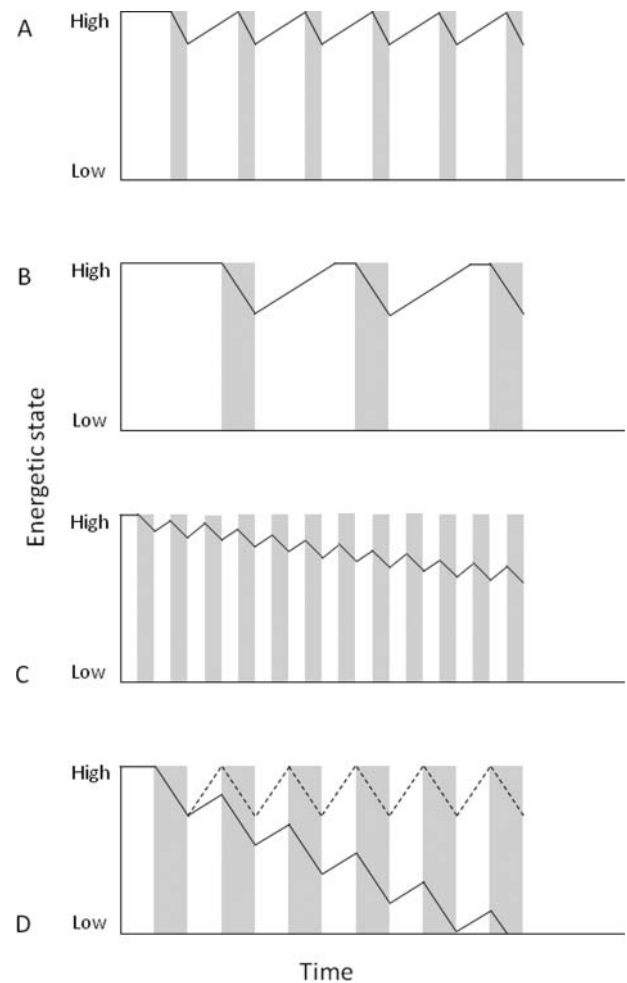


Figure 1. Expected changes in energetic state (lines) with autocorrelated changes in the frequency ( $p$ ) and duration ( $d$ ) of periods when a forager does not have access to food (shaded bars): (A) periods of resource scarcity are infrequent and short ( $p = 0.25$ ;  $d = 1$ ); (B) periods of access (and no access) to food are twice the value as in A ( $p = 0.25$ ;  $d = 2$ ); (C and D) periods of resource scarcity are the same as in A and B, but with higher frequency of occurrence ( $p = 0.5$ ;  $d = 1$  and  $2$ , respectively). The duration of periods with food ( $f$ ) is 1 (C), 2 (D), 3 (A) and 6 (B), respectively. When periods of resource scarcity are infrequent, foragers can regain their maximum energetic state (A, B). But when those periods are more frequent, individuals cannot recover their energetic state unless they reduce vigilance in order to forage more efficiently (dashed line).

durations of resource shortage deplete energy reserves and foragers can only recoup their state by increased foraging rates during favourable periods (dashed line in D, less vigilance). Whether energetic state at the end of the experiment varies only with the proportion of time spent in resource-poor conditions, or as well with the duration of periods with resource shortage or abundance, will depend on the degree to which foragers can compensate depleted energy reserves by increasing foraging speed or efficiency during rich time intervals.

We conduct a test of risk-allocation theory that meets these criteria. We manipulate both the duration and proportion of time that a small arthropod, *Folsomia candida*, is exposed to food-rich versus no-food conditions. We assess survival and reproductive rates of animals living

under the different regimes as surrogate estimates of the animals' energetic state. Animals in a low energetic state should have lower reproduction, and possibly lower survival and offspring quality, than animals in a higher state. We complete the experiment by then assaying the animals' choice between rich and risky versus poor and safe habitats.

## Methods

### Study population

We obtained a laboratory culture of *F. candida* Willem (Collembola: *Isotomidae*) from an established research population (laboratory of Dr G. Boiteau, Fredericton, New Brunswick, Canada). *F. candida* is a globally abundant, parthenogenetic, soil-dwelling hexapod (Fountain & Hopkin 2005; OECD 2009). As all individuals within a population can be considered the same, energetic state can be tracked through the mean values of reproduction and survival (Croua & Cazes 2003).

*F. candida* lacks pigments and external photoreceptors (Fountain & Hopkin 2001, 2005; Fox et al. 2007), the absence of which enables habitat choice to be quantified under full light. *F. candida* is, nonetheless, highly sensitive to other external stimuli and is easily cultured in the laboratory (Fountain & Hopkin 2005). *F. candida*'s small body size and the absence of a desiccation-resistant cuticle (Fountain & Hopkin 2005) make it highly susceptible to dehydration. Prolonged exposure to dry conditions causes negative physiological effects, including reproductive failure, and if long enough, death (Bayley & Holmstrom 1999). Individuals exposed to mixtures of moist versus dry or hazardous soils migrate until they encounter a moist habitat (Fountain & Hopkin 2001; Hilligsøe & Holmstrom 2003; Krogh 2009). Although *F. candida* is capable of physiological adjustments to mitigate the effects of drought stress; these processes are metabolically costly (Bayley & Holmstrom 1999; Hilligsøe & Holmstrom 2003) and require considerably more time than the habitat assessments (48 h) we concentrate on here.

We reared animals according to ISO (1999) and Environment Canada (2007) standard protocols and maintained populations in sealed, transparent plastic chambers with a 1-cm-thick substrate of 9:1 plaster of Paris (MSDS 00071008001) and activated charcoal (Laboratory grade, BIN:81255-03). We maintained laboratory cultures consisting of ~300 hatched animals in constant darkness at room temperature (mean = 21 °C; SE = 0.5 °C) and fed animals *ad libitum* yeast pellets (Fleischmann's® active dry yeast, *Saccharomyces cerevisiae*) weekly. We saturated the chambers with distilled water at feeding time and allowed them to aerate for five minutes.

We created new age-synchronized cultures for the experiments by introducing adults from multiple stock cultures into unoccupied growth chambers and allowed them to lay eggs on the smoothed substrate for 48 h. We carefully moved eggs found with the aid of a binocular dissection microscope (25–44 × magnification) to new chambers with wax-coated specimen pins. Eggs hatched after 7–10 days. Juveniles were then allowed to grow to

reproductive maturity (21–24 days) while we renewed their food and re-moistened the chambers weekly.

### Manipulating energetic state

We transferred a minimum of 30 Collembola from the synchronized rearing chambers into sterile 100-mm-diameter polystyrene disposable Petri dishes. Counting mobile animals during repeated transfers was challenging; therefore, the actual number of animals in some dishes was somewhat higher than the targeted density. We added and removed food according to treatment. Gut turnover in *F. candida* is approximately 24 h (Hopkin 1997); therefore, we established 16-day treatments that varied the proportion ( $p$ ) of days during which food was absent and the number of consecutive days that the animals were deprived of ( $d$ ), or received ( $f$ ), food ( $p=0$  [ $d=0$ ,  $f=16$ ], 0.25 [ $d=1$ ,  $f=3$ ; 2,  $f=6$ ; or 4,  $f=12$  days], 0.50 [ $d=1$ ,  $f=1$ ; 2,  $f=2$ ; or 4,  $f=4$ ; days], or 0.75 [ $d=3$ ,  $f=1$ ; 6,  $f=2$ ; or 12,  $f=4$  days]). Manipulations thus corresponded with treatments that maintained either the duration of days without food ( $p = 0.25$  and  $0.5$ ), or the number of days with food ( $p = 0.5$  and  $0.75$ ), while varying  $p$ . All treatments ended with periods without food. Controls ( $p = 0$ ) were fed daily and were used to verify treatment effects on the mortality, reproduction, and subsequent recruitment of offspring, not to test for differences in  $p$  or  $d$  on habitat selection. We replicated each treatment five times during winter 2014 (24 February to 3 April), and again in spring 2014 (19 March to 29 April; 100 populations in total).

We maintained 100% humidity by pipetting 1000  $\mu$ l of distilled water (100–1000  $\mu$ l Mline® pipette) daily into the periphery of each dish. We recorded the number of clutches and the number of living animals during this time in order to gather information on fitness correlates and thus the energetic state of individuals in the treatment populations. We then removed all eggs in order to avoid altered energetic states caused by cannibalism and recruitment into the treatment populations. We were concerned that some animals may have been injured during the initial transfer; therefore, we replaced animals that perished (or escaped from open dishes while we removed eggs) on days 1–7 using residual subjects from the synchronized stock population. We assumed that the number of dead and escaped individuals would be sufficiently small such that the introduction of a few new animals would not alter a population's mean energetic state. After day 7, we counted the number of animals that escaped or died, but did not introduce new animals that would have insufficient time to achieve the mean energetic state of the treatment population.

### Habitat selection

We transferred all *F. candida* in each dish at the end of the feeding treatments to a new Petri dish where they could choose between two habitats of equal size: an arid food-rich habitat (with an overabundance of yeast pellets but risk of mortality through desiccation; hereafter rich and

risky), and a moist habitat lacking food (poor and safe). We created the two habitats by dividing the substrate into two equal parts with a 0.5 cm × 0.5 cm moisture barrier (Perma all-purpose, all-temperature bonding material, ID 02-0200993). We then filled the habitat-selection Petri dishes with the same plaster of Paris and charcoal mixture as in the feeding treatments, thoroughly dried the substrate, and recorded the weight of each chamber.

We created the safe habitat by re-moistening one-half of each dish with distilled water with a micropipette in order to attain 50% saturation. A 50% saturation level yields 100% survival at 24 h (online Appendix 1). We created risky habitat by adding only enough distilled water in order to ensure high survival through the 1-h period during which we intensely monitored habitat selection (8% saturation, animals exposed to this level for longer periods had low survival, online Appendix 1).

We spread nine yeast pellets haphazardly throughout the rich and risky side, and none on the safe and poor side (*F. candida* can detect and travel to food sources at a distance of 25 mm, Auclerc et al. 2010). We then placed the animals along the midline of each habitat-selection dish with the use of a paper funnel and camel-hair paintbrush. We counted the number of animals occupying the poor and safe habitat at 10-minute intervals to 60 minutes, then converted these values to proportions in order to accommodate differences in the total number of animals among dishes. *F. candida* can fully explore a Petri dish within 10 minutes (Auclerc et al. 2010); therefore, the 1-h trial presented individuals with more than ample time to assess and select habitat according to their energetic state. Even so, we continued to count the number of individuals occupying the poor and safe habitat at 2, 3, 4, 24, and 48 h after their introduction. Analyses of these data yielded qualitatively similar results to those collected during the first hour of observation (online Appendix 1).

### **Reproduction and recruitment**

We searched all dishes for egg masses at both the 24-h and 48-h intervals and recorded the number of clutches within each habitat. We used these correlates of fitness to quantify the relative energetic states of adults exposed to the different treatments (Crouau & Cazes 2003). We supplemented this test in the second set of replicates by counting the number of offspring recruited during the 48-h risk-allocation trial. We discarded the adults, added distilled water and yeast pellets to create a uniformly moist and rich substrate for juvenile Collembola, sealed the dishes with parafilm to maintain humidity, and counted all surviving offspring 21 days later using the floatation method described by Hopkin (1997). We photographed the Collembola within each dish using a Nikon D3200 digital camera, and then displayed the images on a large computer monitor for counting.

### **Experimental predictions**

#### *Mortality during feeding treatments*

If  $p$  determines the energetic state at the end of the experiment, and if the energetic state influences survival, then

survival in our *F. candida* populations should decline with the proportion of time that the animals were deprived of food. Similarly, if duration ( $d$ ) also determines the energetic state, then mortality should increase with the length of no-food periods and especially so at  $p = 0.75$  (when  $d = 3, 6, \text{ or } 12$ ).

#### *Reproduction during feeding treatments*

If animals in a high energetic state lay more eggs, and  $p$  determines energetic state in *F. candida*, then mean fecundity should decline with the proportion of time that animals existed without food. Additionally, if duration also determines the energetic state, then populations exposed to rapid switching between environmental conditions should have higher mean fecundity than populations living in environments with long periods without food (with equal  $p$ ).

#### *Mortality during habitat selection*

Mortality during habitat selection should increase with  $p$  or  $d$  if animals fail to optimize their choices and movements between the safe and food-rich habitats. Differences in mortality by treatment should disappear if animals feeding in the rich habitat retreated to the safety of moisture before their survival was compromised.

#### *Reproduction during habitat selection*

If energetic state determines fecundity and recruitment, then individuals exposed to rapid rates of switching, or infrequent periods without food, should produce more clutches and higher-quality eggs while selecting habitat. After the trial, these treatments would also have the highest offspring recruitment. If animals in a high energetic state prefer the poor and safe habitat, then this habitat should contain more clutches and eggs than the rich and risky habitat.

#### *Habitat selection*

The theory is somewhat ambivalent on whether the proportion or duration of rich and poor conditions should determine habitat choice. Consequently, we designed the treatments so that we could compare three different proportions of time with and without food ( $p = 0.25, 0.5, 0.75$ ), while varying the duration of periods when food was absent or present. Analysis of  $p = 0.25$  versus  $p = 0.5$  controlled  $d$  (1, 2, 4) while varying  $f$  (1, 2, 3, 4, 6, 12). Analysis of  $p = 0.5$  versus  $p = 0.75$  controlled  $f$  (1, 2, 4) while varying  $d$  (1, 2, 3, 4, 6, 12).

### **Statistical analysis**

#### *Mortality and reproduction*

We anticipated that the estimates of mortality and fecundity would not fit a normal distribution. Therefore, we used a set of Kruskal–Wallis  $H$ -tests (hereafter, K–W) to determine if there were significant differences in these

Table 1. Summary of per cent mortality and escape, number of clutches, mean fecundity, and survival of 100 *F. candida* populations living in Petri dishes during a 16-day feeding trial ( $N = 10$  for each estimate).

Treatment*	% Mortality	% Escape	Mean number of clutches per day	Mean number of eggs**	Mean number of survivors
(1) $p = 25\%$ , $d = 1$ , $f = 3$	7.0	3.6	2.59	269.6	30.2
(2) $p = 25\%$ , $d = 2$ , $f = 6$	4.4	8.7	2.70	172.2	29.8
(3) $p = 25\%$ , $d = 4$ , $f = 12$	5.0	6.3	2.52	50.2	30.0
(4) $p = 50\%$ , $d = 1$ , $f = 1$	5.7	10.3	2.08	26.06	30.0
(5) $p = 50\%$ , $d = 2$ , $f = 2$	7.6	6.0	2.13	79.2	30.2
(6) $p = 50\%$ , $d = 4$ , $f = 4$	3.0	8.46	1.53	79.2	29.9
(7) $p = 75\%$ , $d = 3$ , $f = 1$	4.4	15.2	1.59	156.8	29.7
(8) $p = 75\%$ , $d = 6$ , $f = 2$	8.4	7.0	1.20	32.4	29.8
(9) $p = 75\%$ , $d = 12$ , $f = 4$	5.6	19.9	1.44	45.2	30.1
(10) Control	6.6	9.8	2.95	195.0	30.5
Grand mean $\pm$ SD	5.77 $\pm$ 1.57	9.53 $\pm$ 4.54	2.07 $\pm$ 0.58	110.59 $\pm$ 78.42	30.02 $\pm$ 0.23

\* $p$  = proportion of days without food;  $d$  = number of consecutive days without food;  $f$  = number of consecutive days with food.

\*\*Counted from clutches at the end of day 16.

metrics among treatments and the control. K–W tests were appropriate as they resolve non-homogeneous variances that might not be remedied by transformations (Stam et al. 1996). We used pairwise comparisons to identify which treatments were responsible for significant differences in these estimates of “fitness”. We used a one-tailed paired  $T$ -test to assess whether more eggs were laid in the safe than in the risky habitat.

#### Habitat selection

We began our analysis by searching for time-dependent patterns of habitat preference that we obtained at 10-minute intervals with repeated-measures analyses of variance (ANOVAs). We treated dishes as the within-subjects effect and used the analysis to evaluate whether the arcsine transformed proportion of animals occupying the poor but safe habitat depended on the treatment. Our data violated the sphericity condition for repeated measures; therefore, we analysed the time-averaged data, and then confirmed that result by using only data collected at the 60-minute time interval. We used two different  $2 \times 3$  ANOVAs to assess whether habitat selection was best determined by the proportion of time and number of days without food ( $p = 0.25$  vs.  $p = 0.5$ ,  $d = 1, 2$ , and 4), or

the proportion of time and number of days with food ( $p = 0.5$  vs.  $p = 0.75$ ,  $f = 1, 2$ , and 4).

## Results

### Mortality during feeding treatments

The number of surviving *F. candida* during the feeding treatments was high, with a mean mortality of only 5.8% (Table 1); the number of dead Collembola did not vary significantly among treatments and the control (K–W test,  $\chi^2_9 = 3.55$ ,  $P = 0.94$ , Table 2). The number of escaped Collembola over 16 days was higher with a mean value of 9.5%, but again, did not vary significantly among treatments and the control (K–W test,  $\chi^2_9 = 9.00$ ,  $P = 0.44$ , Tables 1 and 2). The ability of these effects to change the population density was neutralized by our addition of replacement animals during the first seven days of the treatment period (the mean number of animals entering the risk-allocation trial =  $30.02 \pm 0.79$ ).

### Reproduction during feeding treatments

As predicted, well-fed *F. candida* ( $p = 0, 0.25$ ) produced, on average, more clutches each day (Table 1) than did

Table 2. Summary of Kruskal–Wallis tests evaluating (a) mortality and escape during the 16-day feeding treatment; (b) reproduction during the feeding treatment, number of clutches and number of eggs produced on day 16; (c) reproduction during the risk-allocation trial; and (d) offspring survival until adult age (21 days).

Analysis*	$df$	$\chi^2$	$P$
(a) Mortality among treatments ( $N = 100$ )	9	3.55	0.94
Escape among treatments ( $N = 100$ )	9	9.0	0.44
(b) Number of clutches among treatments ( $N = 100$ )	9	47.22	<0.001
Number of eggs among treatments ( $N = 100$ )	9	12.76	0.174
(c) Number of clutches among treatments ( $N = 100$ )	9	38.84	<0.001
(d) Recruits among treatments ( $N = 100$ )	9	28.48	<0.001
Recruits among proportion of days without food ( $N = 100$ )*	3	21.08	<0.001

\*Proportion included as a nominal variable.

Table 3. Summary of mortality and clutch production at 48 h, and selection of safe habitat at 60 minutes, by 100 populations of *F. candida*.

Treatment	Mean # of clutches ( $N = 10$ )	Mean # of dead animals ( $N = 10$ )	Proportion in safe habitat at 1 h
(1) $p = 25\%$ , $d = 1$ , $f = 3$	5.5	0.5	0.57
(2) $p = 25\%$ , $d = 2$ , $f = 6$	7.2	0.9	0.63
(3) $p = 25\%$ , $d = 4$ , $f = 12$	6.3	0.1	0.54
(4) $p = 50\%$ , $d = 1$ , $f = 1$	3.9	1.1	0.54
(5) $p = 50\%$ , $d = 2$ , $f = 2$	11.0	0.5	0.54
(6) $p = 50\%$ , $d = 4$ , $f = 4$	5.6	1.2	0.53
(7) $p = 75\%$ , $d = 3$ , $f = 1$	2.4	0.7	0.39
(8) $p = 75\%$ , $d = 6$ , $f = 2$	1.6	6.5	0.45
(9) $p = 75\%$ , $d = 12$ , $f = 4$	0.4	3.6	0.36
(10) Control	4.4	3.3	0.66
Grand mean $\pm$ SD	4.83 $\pm$ 2.9	1.84 $\pm$ 1.92	0.52 $\pm$ 0.09

animals in other treatments (K–W test,  $\chi^2_3 = 77.93$ ,  $P < 0.001$ , Table 2). Control animals, and those receiving food for 75% of the time ( $p = 0.25$ ), produced the most clutches while individuals that were mostly food deprived tended to produce fewer clutches (Table 1). These results were confirmed when we repeated the analysis on ungrouped treatments. Treatments with  $p = 0.75$  (and treatment 6,  $p = 0.5$ ,  $d = 4$ ) yielded fewer clutches per day than treatments with  $p = 0$  or 0.25 (*post hoc* pairwise comparisons; overall K–W test,  $\chi^2_9 = 47.22$ ,  $P < 0.001$ , Tables 1 and 2). Despite differences in the number of clutches produced, there were no significant differences among treatments in the number of eggs laid on day 16 (K–W test,  $\chi^2_9 = 12.76$ ,  $P = 0.17$ ).

### Mortality during habitat selection

Mortality during the risk-allocation trial was low (Table 3). All animals survived through the 60-minute trial and only 183 of the 3005 Collembola perished by 48 h. More animals appeared to die in the poor and safe habitat (103) than in the rich and risky habitat (80), but this difference was not statistically significant.

### Reproduction during habitat selection

The vast majority of clutches (482 of 492) was located in the poor and safe habitat (paired *T*-test:  $T_9 = 8.15$ ,  $P < 0.001$ ). The mean number of clutches laid varied significantly among treatments and the control (K–W test,  $\chi^2_9 = 38.84$ ,  $P < 0.001$ , Tables 2 and 3, and online Appendix 2). These differences were mainly attributable to the treatment with the longest duration of time without food (12 days; this treatment produced significantly fewer clutches than treatments with  $p = 0.25$ , as well as those with  $p = 0.5$  ( $d = 2$  or 4; *post hoc* pairwise comparisons, Table 3).

Well-fed Collembola, as predicted, produced more recruits than Collembola starved for  $p = 0.75$  of the time (K–W test,  $\chi^2_3 = 21.08$ ,  $P < 0.001$ , Table 2). These effects were mainly attributable to the two treatments with the longest durations without food (6 and 12 days,

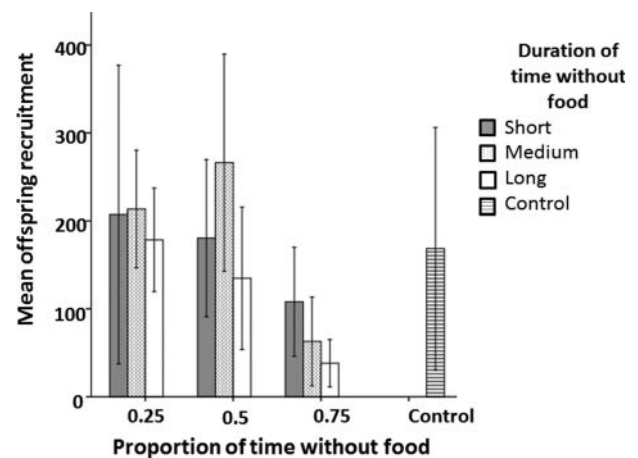


Figure 2. Mean ( $\pm$  SE) recruitment of 100 *F. candida* populations conditioned over 16 days to different frequencies and durations of days without food.

respectively, *post hoc* pairwise comparisons; overall K–W test:  $\chi^2_9 = 28.48$ ,  $P < 0.001$ , Table 2 and Figure 2).

### Habitat selection

Habitat selection by Collembola varied significantly among treatments experiencing different proportions of time without food, but only in the analyses comparing  $p = 0.5$  versus  $p = 0.75$  (Table 4). The relative densities of Collembola within safe habitat were substantially lower for animals starved 75% of the time compared with those starved for 50% of the time (Figure 3). Analyses yielded qualitatively identical results whether based on the time-averaged data or only those collected at 60 minutes. Duration had no significant influence on habitat selection in any analysis. Habitat selection in the Collembola responded primarily to  $p$  and not to  $d$  ( $d$  was identical between  $p = 0.5$  and  $p = 0.75$ ) or  $f$  ( $f$  was different between  $p = 0.25$  and  $p = 0.5$ ).

### Discussion

Risk-allocation decisions are a form of optimal foraging behaviour that depends on the broader context in which environmental risk varies (Lima & Bednekoff 1999;

Table 4. Summary of analyses of variance assessing habitat choice by nine populations of *F. candida* following exposure to differing periods of resource shortage.

Comparison	Source	df	F	P
$p = 0.25$ vs. $p = 0.5$	Model	5	1.27	0.29
	Intercept	1	2814.4	<0.001
	$p$	1	2.06	0.16
	$d$	2	1.50	0.23
	$p \times d$	2	0.63	0.53
	Error	54		
$p = 0.5$ vs. $p = 0.75$	Model	5	4.92	0.001
	Intercept	1	1822.4	<0.001
	$p$	1	18.25	<0.001
	$f$	2	2.11	0.13
	$p \times f$	2	1.06	0.35
	Error	54		

Note:  $p$  = proportion of time without food;  $d$  = duration of time without food;  $f$  = duration of time with food.

Sih & McCarthy 2002). Such decisions can determine whether an animal survives in a stochastic environment or succumbs to either starvation or predation within a given time interval (Brown et al. 1999; Higgison et al. 2012). Our experiments with *F. candida* are consistent with previous studies documenting that the risk-allocation behaviour of foragers emerges through temporal patterns of environmental change influencing energetic state (Ferrari et al. 2009; Sih & McCarthy 2002). Exposing *F. candida* to different feeding treatments forced animals into a variety of energetic states that subsequently influenced their choice of a rich habitat with desiccation stress over a poor, moist one. Populations experiencing frequent and regular access to food selected the safe habitat more often, while animals deprived of food for 75% of the time

selected the rich and risky habitat despite danger of mortality through desiccation.

It is nevertheless difficult to attribute differences in habitat selection to only energetic state. Animals in treatment 3, for example, endured four consecutive days without food before choosing habitat and nevertheless expressed similar variation in habitat choice as did animals in treatment 1 (one day without food). The same was generally true of comparisons between treatments 9 (12 days without food) and 7 (3 days without food). It is tempting to conclude that the expectation of food deprivation ( $p$ ) may play an important role in the choice between a safe but poor habitat and a risky rich one. It may be more likely, however, that the animals experienced an energetic threshold (between 50% and 75% food deprivation) below which they were incapable of regaining their state and were thus forced to forage in rich and risky habitat (Brown et al. 1997). Repeated or prolonged bouts of food scarcity, interspersed with relatively short periods of recovery (as for  $p = 0.75$ ), are more likely to reduce an animal's cumulative energetic state than are equal periods of food scarcity in an environment with more frequent foraging opportunities (Figure 1).

Estimates of the number of clutches and recruits produced by animals exposed to different food versus no-food regimes confirmed our assumption that those feeding treatments altered energetic states. Well-fed *F. candida* produced more clutches than did poorly fed animals. They were also more selective in oviposition habitat, and higher recruitment success suggests that they likely produced higher quality eggs than did poorly fed individuals. These results are consistent with the interpretation that reproductive success should reflect changes in environmental condition (Ludwig & Rowe 1990), and especially so in *F. candida* (Staempfli et al. 2007; Tully & Ferriere 2008). It is thus reasonable to conclude that differential habitat selection in our experiments was caused by adaptive risk allocation in response to depleting energy reserves.

Oddly, differences among treatments in the number of clutches produced over the 16-day feeding period were not mirrored by similar differences in the total number of eggs produced on day 16. We attribute this anomaly to reproductive asynchrony among populations. *F. candida* intersperses short 36-h bursts of egg laying with long (~8 days) non-reproductive periods during which they acquire resources and moult to the next instar (Fountain & Hopkin 2005). Females oviposit eggs into communal clutches during each reproductive phase. It is thus likely that differing numbers of females reproduced daily in each population. This probability was enhanced by our initial accumulation of eggs produced over a period of 48 h in order to create "synchronized" populations. Differences in reproductive output were thus more likely to be reflected in the number of clutches produced over 16 days, than in the number of eggs produced in only 1 day. Regardless, the significant influence of food treatments on the number of clutches, as well as offspring recruitment, is consistent with our predictions of risk allocation and confirms other studies demonstrating that habitat selection mirrors habitat differences in fitness (Morris & Davidson 2000).

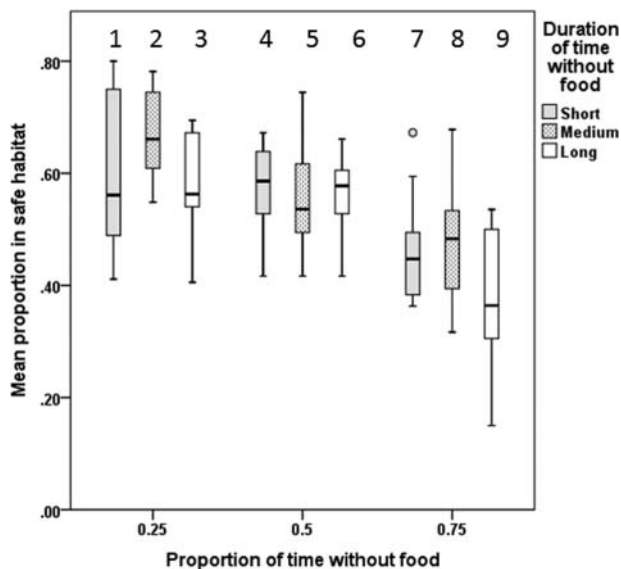


Figure 3. Box plots illustrating that *Folsomia candida* populations exposed to resource scarcity for 75% of the time in a 16-day experiment were less likely to occupy a safe food-poor habitat than were animals exposed to food for a greater proportion of time. Numbers above box plots identify treatments (as in Tables 1 and 3).



Our results dispute the claim that the predictions of the original risk-allocation hypothesis are inaccurate (Beauchamp & Ruxton 2011; Higginson et al. 2012). Inconsistencies in tests of risk-allocation theory appear less likely to have been caused by shortcomings of the hypothesis itself than by an imperfect fit between test conditions and the theory's key assumptions (Ferrari et al. 2009; Higginson et al. 2012; Bednekoff & Lima 2011). Our work demonstrates that tests of risk allocation may often require rather complicated experimental designs in order to winnow the data to their appropriate causes and effects. Our research similarly opens the door conjoining risk allocation and habitat selection.

The demonstrated differences in habitat choice among populations experiencing depleting energy resources add to the growing evidence that habitat selection reflects innate habitat quality (Olsson et al. 2002; Knight et al. 2008). Foraging behaviours provide insight into the condition of individuals, habitats, and communities (Kotler et al. 2007). Because individuals require energy to survive and reproduce, there is an intrinsic link between foraging behaviour with fitness that we can use to detect stochastic (Morris 2001) and habitat differences (Morris & Davidson 2000) in environmental condition and quality. Monitoring changes in risk-allocation behaviour can thus inform us of changes in the foraging profitability of different habitats (Kotler et al. 2007; Morris & Davidson 2000). Detecting those changes through the foraging behaviour of individuals may allow wildlife and conservation managers to counteract habitat change before the abundance and distribution of threatened populations are irrevocably altered (Kotler et al. 2007).

### Acknowledgements

We thank B. Kotler for kindly inviting us to contribute to this special edition celebrating the science and life of Karen Embar. We remember Karen's short visit to our laboratory and research group, and her spirited discussions on evolutionary ecology with great fondness. Our collective science is poorer through her untimely passing. We thank Dr G. Boiteau for generously providing our lab with stock populations of *F. candida*, as well as D. Durston, D. Start, and our Evolutionary Ecology Research Team for contributing their time and effort to pilot studies assessing the potential of habitat selection by *F. candida*. The manuscript was improved by candid suggestions from B. Kotler and anonymous reviewers. We gratefully acknowledge support provided to A. Bannister by Lakehead University and the Northern Lake Superior Research Award.

### Disclosure statement

No potential conflict of interest was reported by the authors.

### Funding

This research was supported by Canada's Natural Sciences and Engineering Research Council [grant number 116430-2013].

### Supplemental data

Supplemental data for this article can be accessed here.

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