



Experience influences settling behaviour in desert isopods, *Hemilepistus reaumuri*

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Habitat quality, and the levels of habitat variables that are associated with good habitat, can vary between years. Therefore, animals that are able to adjust their habitat selectivity should enjoy higher fitness. I examined the use of experience in habitat selection during natal dispersal in *Hemilepistus reaumuri*, a monogamous, semelparous desert isopod. Young from the previous year emerge in the spring and walk from a few to over one thousand metres before establishing burrows or settling in already established burrows. Isopods were held in outdoor pens for 7-day priming treatments, then moved to new pens and tested for settling 4 days later. Perceived habitat quality was defined as the fraction of isopods settling in each pen during its use in the 7-day priming treatments. Settling was tested as a function of the change in perceived quality isopods experienced. Settling was significantly positively correlated with change in perceived quality, suggesting that experience is used to prime habitat selection during dispersal, and that the effects of experience last at least a few days in desert isopods. Time of year also had a significant positive effect on settling. The effect of change in perceived quality was stronger than the effect of perceived quality in the final pen. If changes in habitat are used to calibrate settling decisions, longer dispersal distances may be needed to allow for habitats to be compared. Use of experience to regulate settling may also affect the population dispersal response to habitat change.

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Natal dispersal (sensu Greenwood 1980) may be the behaviour that is most critical to predicting the effects of habitat loss or change, because many models and predictions of the persistence of subdivided populations rest on untested assumptions about movement between habitat patches (Kareiva & Wennergren 1995; Johst & Brandl 1997; Ruckelshaus et al. 1997). Dispersal is poorly understood compared with other life-history variables, and the role of experience in regulating dispersal behaviour is even less well understood (Stamps & Krishnan 1999). Increasing attention is being paid to the role of experience in the foraging (Dukas 1998) and settling (Reed et al. 1999) decisions that animals can and do make. Because successful dispersal ends in settling, investigations of the settling decisions that animals make during dispersal can aid our understanding of natal dispersal patterns.

During natal dispersal, individuals may be viewed as foraging for the highest-quality breeding sites. How can

use of experience improve an individual's settling decisions? If the distribution of habitat quality, or the habitat features that are good predictors of reproductive success, vary between generations, then settling decisions based on an inflexible expectation of habitat quality, or a hard-wired settling response to a threshold value of habitat features, should lead to lower fitness than flexible decisions, which can start from an initial, perhaps genetically influenced, likelihood of settling that is adjusted based on experience during movement. Models have shown that the ability to use experience to regulate habitat selection can increase fitness under a wide range of dispersal costs and habitat variability (Baker 1998; Schjørring 2002). The use of experience allowing selectivity to adapt to current conditions has been termed priming, and has been examined in hymenopterous parasitoids (Turlings et al. 1993) and other insects (Mark 1982). During priming, new associations are not formed through learning, but rather are shaped by experience based on the level of responsiveness to cues already associated with a decision, in this case settling.

Priming may be especially important when the mean of some habitat feature that is correlated with reproductive

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success varies between years, such as rainfall, temperature, or any landscape features affected by those variables. In this case, individuals with a fixed settling response to some level of the habitat feature will either be too choosy or too accepting of habitat in years with low or high values of the habitat variable, respectively. Increased choosiness leads to longer dispersal distances and exposure to whatever risks are present during movement (Baker & Rao 2004), whereas reduced selectivity leads to shorter dispersal distances and perhaps reduced future reproductive success (Stephens 1989).

The influence of priming on the likelihood of settling during natal dispersal has not been studied. Although experience has been shown to influence location of mates (Prokopy et al. 1989) or hosts (Papaj 1986) in insects, studies of experience and movement in vertebrates have focused on breeding dispersal, primarily in birds. For example, breeding success is positively correlated with site fidelity in lesser kestrels, *Falco naumanni* (Tella et al. 2001), white-chinned petrels, *Procellaria aequinoctialis* (Bried & Jouventin 1999), American robins, *Turdus migratorius*, brown thrashers, *Toxostoma rufum* (Haas 1998) and red-winged blackbirds, *Agelaius phoeniceus* (Beletsky & Orians 1991), but not in Cassin's auklets, *Ptychoramphus aleuticus* (Pyle et al. 2001) or wild turkeys, *Meleagris gallopavo* (Badyaev & Faust 1996). Breeding success of conspecifics is correlated with site fidelity in cliff swallows, *Petrochelidon pyrrhonota* (Brown et al. 2000) and collared flycatchers, *Ficedula albicollis* (Doliguez et al. 1999). The emphasis on prospecting prior to movement is appropriate in many cases, especially in socially or colonially nesting species (Reed et al. 1999), but may also reflect the difficulty of observing and studying foraging during natal dispersal. In some species, juveniles with large home ranges may nest beyond their familiar areas (Anders et al. 1998) or floaters that delay breeding may keep shifting their home range and colonize unfamiliar areas (Shutler & Weatherhead 1994).

In this study, I tested whether experience during dispersal affects selectivity and settling behaviour in *H. reaumuri*. *Hemilepistus reaumuri* is a semelparous, annual isopod found in Old World deserts in North Africa and central Asia that displays monogamy and parental care (Shachak 1980; Linsenmair 1984). Most of their life is spent near a family burrow, from which they make short (1 m, Hoffmann 1985) trips to feed on soil and to deposit faeces at the surface. Starting from late January or February, during a dispersal season that varies from 2 to 6 weeks, young from the previous year emerge from their natal burrows, travel, and search either for suitable sites for establishing new burrows or for existing burrows (Baker 2004). Desert isopods can travel long distances; in one study, individuals commonly moved 250–450 m before settling (unpublished data cited in Warburg et al. 1984), and individuals have been observed to travel over 1 km (Hoffmann 1989; Baker 2004). The likelihood of a burrow being started by either sex varies during the season: early in the season, most burrows are initiated by females, with pair formation following acceptance of a male into the burrow; later in the season, males are as likely to start burrows that are joined by females

(Linsenmair 1984; Baker 2004). Mortality is significantly higher during movement than after settling (Baker & Rao 2004). Habitat variables such as shrub density and soil moisture as well as the density of previously successful burrows all influence settling and selection of high-quality habitat, which is critical to family survival and fitness (Shachak & Brand 1988; Baker et al. 1998).

I examined whether the use of experience by desert isopods during natal dispersal influences their habitat selectivity and their willingness to settle in a given patch. Isopods were held in outdoor enclosures of varying perceived quality, as defined by the settling behaviour of different isopods in those enclosures, and then transferred to new enclosures of varying levels of perceived quality. If previous experience affects selectivity, individuals should be more likely to settle in a given patch that has a higher perceived quality than the patch they had previously experienced, independently of the perceived quality of the current patch.

METHODS

Study Area

The experiments took place on a loess plain (Sde Zin) in the central Negev, Israel (34°46'E, 30°50'N). The study area is 500 m above sea level, and the average annual rainfall is about 90 mm (range 34–167 mm).

Experiment

To examine the role of previous experience in isopod habitat selection, I collected isopods at emergence from their burrows, then sexed, weighed and marked them and placed them in outdoor pens (3 × 3 m²) for a 7-day priming treatment. Following the priming treatment, I randomly assigned individuals from each pen to one of three groups and placed each group in a new pen for 4 days. I censused each pen to determine whether isopods had settled or were still on the surface (Fig. 1). Although the pens greatly constrained the range of isopod movements, they contained all of the habitat components normally encountered during dispersal, such as old and new burrows, shrubs, scorpion burrows and other isopods. The density of isopods added to each pen during the priming treatments (5–6.7/m²) was about half the density of emerging isopods in the same plain during the year of the study ($\bar{X} \pm \text{SD} = 13.6 \pm 6.9$; Baker 1998). Since emergence takes place throughout the dispersal period, the densities in the pens during the priming treatments were probably higher than in the open field, but the density in each settling test pen (1.6–3.9/m²) was probably lower than that of unsettled isopods in the open field. The pens may have influenced settling behaviour aside from constraining the variation in habitat experienced, so I made comparisons only between pens, and not between enclosed and open-ranging isopods. The durations of priming and settling treatments were chosen so that the combined duration of both treatments matched the observed mean time before settling of 10–13.7 days over 2 years of a related

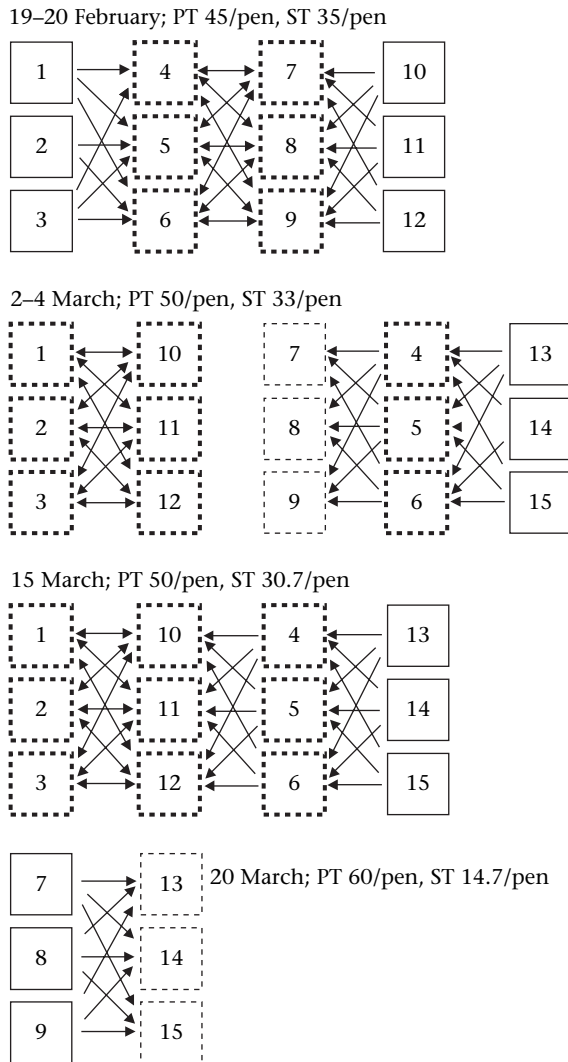


Figure 1. The design of the learning experiment. Direction of transfer among pens indicated with arrows. Pens are identified by number, and the average numbers of isopods per pen at the start of each priming treatment (PT) and collected at the end of each settling trial (ST) are included. Pens used only for priming are drawn in solid lines, those used for settling are drawn in dashed lines, and those used for both priming and settling are in bold dashed lines.

study (Baker 2004), and because a pilot study indicated that more settling took place after 4 days than after 2 days following transfer between pens. Some isopods had already settled at the end of the 7-day priming treatment. I tested for the effect of settled or unsettled state on subsequent settling during the settling trial using chi-square on the pooled group of all isopods completing the settling trials, to maximize the chance of observing any potential effect of settlement during the priming treatment on subsequent behaviour. Four rounds of priming and settling testing were completed, with the number of pens determined by the availability of emerging isopods. I placed 45–60 isopods in each pen at the start of each priming treatment, and placed equal numbers of survivors from the first treatment (14.7–35) in different pens for the second treatment. Because some isopods died or disappeared during the

priming treatments, I pooled isopods from the first and third priming rounds and used fewer pens to test for settling behaviour (Fig. 1). All settled and unsettled isopods were collected and removed at the end of each treatment, and newly collected emerging isopods were used each round. I introduced 1915 isopods to 15 pens for 39 total priming treatments over the course of the study, and I collected 837 isopods at the end of all the settling tests. All burrows were filled in at the end of each priming and settling treatment before new introductions of isopods, then capped with a snail shell larger than the diameter of the burrow. While it is possible that isopods could recognize burrows from earlier replicates, this was unlikely because no visible physical landmarks of the burrows remained. Isopods use physical landmarks to recognize burrows and are unable to distinguish familiar from non-familiar burrows without encountering burrow residents (Hoffmann 1985), suggesting that they do not respond to chemical residues from the burrows themselves. Each group was initially set up to receive one of three levels of manipulation of soil moisture, a feature known to influence settling behaviour in this species. (Baker et al. 1998; Brandwine & Shachak 1998). However, because heavy rains took place following manipulation of soil moisture and none of the replicates showed any response to the irrigation treatment (results not shown), I used the settling behaviour of the isopods during the priming treatments as a baseline measure of perceived habitat quality.

I assigned an index of perceived habitat quality to each pen, defined as the cumulative proportion of isopods settling in that pen during the 7-day priming treatments pooled over all replications. Because the perceived habitat quality of a given pen during the settling tests was determined by the behaviour of different isopods during their priming treatments, the perceived quality of a pen during a settling test was independent of isopods' behaviour in that pen. A total of 15 pens were used two or three times each for a total of 39 priming treatments. This allowed testing for consistency of perceived habitat quality for individual pens, using a mixed model of the effect of time during the season and pen on the proportion of isopods settled at the end of each priming treatment.

Each isopod experienced two levels of perceived habitat quality during the experiment; that of its priming pen and that of its settling test pen. The difference in perceived habitat quality between the settling test pen and the priming pen, referred to as the change in habitat, was used to determine whether isopods use experience to adjust their likelihood of settling. For example, an isopod that spends 7 days in a pen with a perceived habitat quality of 0.3, then is tested for settling in a pen with a perceived habitat quality of 0.5 would be counted as experiencing a change in habitat of +0.2. I calculated the perceived quality of each settling test pen independently of the isopods in the settling tests, but the change term was not completely independent, because a small fraction of the perceived quality of the priming pen was due to the settling behaviour of the group moving from that priming treatment to its settling test pen.

The statistical units for analysing settling as a function of change in habitat were the 15 pens used to test for

settling behaviour over the course of the study. A total of 837 individuals in 115 groups of 1–14 isopods, three from each of the 39 priming treatments (minus two where no survivors were found after the settling test), completed the settling trials. In addition to any effect due to the experimental manipulation, the settling behaviour of individual isopods was probably affected by other isopods in the same pen, and possibly by other characteristics of the pens themselves. For each pen, I performed a regression of the arcsine-transformed proportion of each group settling on the change in perceived habitat quality experienced by that group and the date of the settling test. I tested the distribution of slopes for goodness of fit to the normal distribution, but because of small sample size, I also tested the distribution of slopes using a signed-ranks test as well as a *t* test to determine whether its mean was greater than zero. A mean greater than zero for the distribution of regression slopes is predicted if isopods increase their likelihood of settling when they experience an increase in perceived habitat quality.

To quantify the effect of previous experience relative to that of the perceived habitat quality of the final pen, I performed a linear regression of the arcsine-transformed proportion of isopods that settled on the perceived quality of the final pen, the change in perceived quality and the number of days since 1 January of the settling test on the 115 groups of isopods that were moved between pens. Groups of isopods were not independent of each other, because each settling trial included three or six groups inside a single pen, but this analysis can still be used to examine the relative impact of the change versus the perceived habitat quality of the final pen.

RESULTS

Perceived habitat quality of individual pens was consistent. Pens differed significantly in the proportions of settled isopods during the priming treatments (ANOVA: $F_{14,23} = 7.3021$, $P < 0.0127$), and date also had a significantly positive effect on settling ($F_{1,23} = 2.8513$, $P < 0.0126$). The state (settled or open) of an isopod at the end of its priming period had no effect on its likelihood of settling during the settling test period (chi-square likelihood ratio test: $\chi^2_1 = 0.486$, $N = 829$, $P = 0.4859$; Table 1), so all individuals collected after the priming treatments were included in later analyses of settling.

Table 1. Settled versus unsettled state at the end of the settling test period as a function of settled versus unsettled state at the end of the experience treatment

Experience treatment	Settling test	
	Unsettled	Settled
Unsettled	496	141
Settled	154	38

Isopods found settled or unsettled at the end of the experience treatment were not more or less likely to settle during the settling trial (chi-square test: $\chi^2_1 = 0.486$, $N = 829$, $P = 0.4859$).

Change in perceived habitat quality was significantly associated with settling behaviour (Fig. 2). The distribution of slopes did not appear to deviate from normality using the Shapiro–Wilk's test of goodness of fit ($W = 0.977$, $N = 15$, $P = 0.916$). The mean \pm SE of the slopes of the within-pen regressions was 1.51 ± 0.43 , which was significantly greater than zero using parametric (one-sample *t* test: $t_{14} = 3.5140$, $P = 0.0017$) or nonparametric tests (Wilcoxon signed-ranks test: $T = 43.5$, $N = 15$, $P = 0.002$). A mean slope greater than zero signifies that isopods were more likely to settle when the change in perceived habitat quality from priming to settling treatments was more positive.

A group-level analysis of settling behaviour of isopods that were moved between pens suggests that the change in perceived quality had a greater effect on settling than the perceived quality level of the final pen (Table 2, Fig. 3). Time of year had a highly significant positive effect on settling, such that isopods were more likely to settle later in the dispersal season. When included in the single model, change in perceived quality had a significant positive relationship with settling, but the perceived quality of the settling test pen was not significantly correlated with settling.

DISCUSSION

Experience influences burrow-site selectivity of desert isopods during dispersal. Isopods that experienced an improvement in perceived habitat quality were more likely to settle in a given pen than those in the same pen who experienced a decline or no change, as evidenced by the significantly positive regression slopes of settling on change in perceived quality. The effect of change in perceived quality was stronger than the effect of the perceived quality of the final pen, further emphasizing the role of experience on the timescale of the present study. The results of the present experiment do not specify the mechanisms of habitat selection or the cognitive learning and memory capacities of desert isopods, nor do they

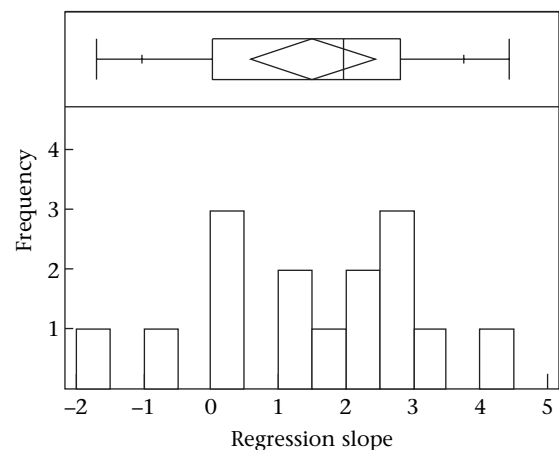


Figure 2. The distribution of slopes (and a normal quantile box plot) of regressions performed within each of the 15 pens in the experiment of settling on the change in perceived habitat quality and the date of the settling trial.

Table 2. Effect of change in preference level, time of season and perceived quality of settling pen on the arcsine-transformed proportion settling

Source	Estimate	df	$F_{1,11}$	P
Intercept	-0.2320		-1.08	0.2841
Change in perceived quality	1.2230	1	3.57	0.0005
Days since 1 January	0.0088	1	3.05	0.0028
Perceived quality of settling pen	0.3336	1	0.99	0.3258
Whole model adjusted R^2	0.2234	3	11.93	<0.0001

The estimates correspond to regression parameters for each factor in the model.

depend on which cues and learning mechanisms were used. However, further work on both fronts is needed to understand the constraints on habitat selection and ultimately the reasons why this and other species move as far and take as long as they do before settling to breed. For instance, if conspecific burrows or nest sites are used as a measure of habitat quality, artificial burrows or nestboxes might be sufficient to stimulate settling. However, if food quality or plant cover is used to assess habitat quality, then more substantial manipulation or management will be required.

The stronger effect of change relative to perceived quality in the final pen raises the more general question of why change in habitat should be used to influence choosiness. One reason might be that changes in habitat are needed to functionally calibrate the cues for a specific season's range of habitat quality. Theoretical and field studies of prospecting (reviewed in Reed et al. 1999; Danchin et al. 2001) have shown that dispersers sample habitat, but they implicitly assume that the value of what is sampled is already known, and that the values of the cues used to select habitat are constant. For example, Doliguez et al. (2002) showed that patches with artificially increased broods attracted more immigrant collared flycatchers. If a prospecting immigrant observed that most of the nests in a patch have two nestlings, how does it know that this level of productivity indicates superior or inferior habitat? The present study indicates that experience can influence an individual's subsequent appraisal of habitat, by using changes and possibly relative levels of habitat variables,

rather than fixed thresholds, to guide settling. Changes in reward or perceived reward are thought to be a primary mechanism for learning to associate conditioned responses to unconditioned stimuli (Menzel et al. 1993), and rules of thumb based on relative improvement or decline have been hypothesized (Ollason 1980) and observed in other foraging contexts (Menzel et al. 1993). However, use of changes in habitat to choose settling sites might incur a sampling cost, in that more habitat must be explored to detect changes and measure variation between patches.

Several theoretical approaches have been developed to understand when use of experience in general, and learning in particular, will aid foraging decisions (MacNamara 1985; MacNamara & Houston 1987; Stephens 1987, 1989, 1993; Mangel 1990, 1993). These models are at least partly applicable to natal dispersal decisions. In general, learning is favoured when the scale of variation in time and space exceeds the capacity of evolved fixed responses to habitat cues to efficiently track optimal habitat, and when variation is low enough within animals' lifetimes, or between the learning and decision times, that learned responses are reliable. Isopods should benefit a great deal from learning during dispersal, because settling is an infrequent decision regarding a variable resource with long-term fitness consequences (Shachak & Brand 1988). Given the variation in distances travelled by dispersing organisms (birds: Paradis et al. 1998; insects: Dingle 1996) and the high costs of dispersal for dispersing or migrating animals in general (Waser et al. 1994; Ward et al. 1998), travelling individuals should use previous experience to influence their settling decisions and the resulting dispersal distances. Increased sampling costs reduce the time that should be devoted to sampling, but use of experience is sometimes favoured even in the face of high sampling costs, such as the loss of a year of breeding in birds (Boulinier & Danchin 1997; Schjørring 2002). The balance of costs of movement and potential benefits of continued searching should vary with time, as predicted by models that include time as a state variable.

Dynamic programming models of optimal foraging when time is limited generally predict that selectivity in this kind of decision, to accept or reject a patch once in a lifetime, should decline as the time horizon approaches (Ward 1987; Mangel & Clark 1988), and this was a specific prediction from a dynamic programming model of isopod

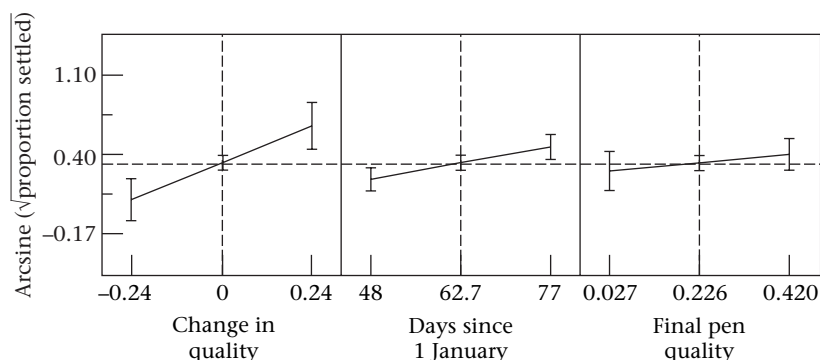


Figure 3. Profiles of predicted arcsine-transformed proportion settled as a function of change in quality, time of season and final pen quality, from the multiple regression. Error bars are 95% confidence intervals around the predicted values.

settling as well (Baker & Rao 2004). Late in the spring the likelihood of hot weather greatly increases the risk of mortality to unsettled isopods, limiting the time available for movement and settling (Linsenmair 1984). As the end of the season approaches, the likelihood of surviving to encounter superior habitat declines. This prediction of reduced selectivity was supported in the increasing likelihood of settling observed in desert isopods later in the dispersal season. The decrease in selectivity later in a limited season is similar to behaviour predicted and observed in parasitic wasps (Roitberg et al. 1993) searching for mates. Searching for habitat during natal dispersal is similar to mate searching in parasitoids in that finding a mate, like isopods' settling, may happen once or only a few times in a parasitoid's lifetime. Not all isopods experiencing a positive change in perceived habitat quality settled during the settling trials, nor should this be expected. Even if settling were based entirely on habitat quality, settling decisions should depend not just on whether the currently occupied patch is better than the previously occupied one, but on the overall mean, variability and autocorrelation of habitat quality, and the time year, which predict the chances of finding a better patch if searching continues.

This study shows that previous experience influences settling in desert isopods in a pattern consistent with expectations from foraging models, but further study is needed to understand both the mechanisms of habitat sampling and the learning or related mechanisms that allow isopods to incorporate experience into their behaviour. The use of isopod settling as a proxy for habitat quality assumes that isopods select superior habitat. Isopods select habitat, although it is not precisely known what features are being directly sampled or how those features influence settling. Isopod population and settling density is correlated with soil moisture content and water runoff (Shachak & Brand 1991), and in two experiments, isopods increased settling in response to supplemental water (Baker et al. 1998). However, they did not settle in open plots with higher soil moisture at depths of 10 and 30 cm (Baker 1998). It is not known whether isopods directly respond to moisture, or to an indirect effect of moisture such as temperature, food quality or shade. Isopods feed during the dispersal season (Baker & Rao 2004), which is one way they might sample habitat. Settling responses could reflect active decisions; however, habitat selection does not require a cognitive choice to function adaptively. For example, if movement through superior habitat is slower, individuals could settle more densely in those areas without changing their settling behaviour. An effect of experience does, however, require a change in response to habitat cues or a change in probability of settling due to the earlier experience. Further study is needed to understand whether that change in sensitivity uses learning and memory, or a simpler behavioural mechanism.

The use of experience observed here may or may not rely on learning, depending on how learning is defined, and on the behavioural mechanisms underlying the observed effect. Dukas (1998) defines learning as 'the acquisition of or change in memory that allows a subject to alter its subsequent responses to certain stimuli'. A change in

settling behaviour as a function of habitat experienced at an earlier time fits the first definition only if it can be demonstrated that memory is involved. For example, since isopods do settle more densely in patches with more successful old burrows, a reliable predictor of new burrow success, and also in patches with more shrubs (Baker 1998; Baker et al. 1998), they could use memory of encounters with old burrows and compare recent and long-term encounter rates, and use any change in encounter rates to influence settling. Manipulation of the cues that influence settling is needed to determine whether memory of those cues influence settling. Memorization of cues may not be a necessary component of habitat experience if, for example, isopods evaluate habitat by integrating the taste of the soil in the current patch with some other longer-term consequence of food quality, such as gut content or body condition, as a way to compare local and global conditions without using memory. Papaj & Prokopy (1989) emphasize the repeatable, gradual and reversible features of learned behaviours rather than using memory as a criterion. Experiments that vary the timing of experience and settling trials are needed to determine how durable and reversible are experience effects on settling, and then the temporal scale of sampling can be compared to the spatial variation in habitat quality and the speed of movement.

The use of experience to influence dispersal and habitat selection can influence the response of populations to habitat loss or change. Many models of the persistence of populations in the face of habitat loss or destruction depend on the movement of individuals to replenish small or subdivided populations. They assume that animals will either disperse similarly before and after habitat change or, even more optimistically, that they will search until an empty site is located (Carroll et al. 1995; Noon & McKelvey 1996). This might be the case, if dispersers are programmed to continue moving until a genetically programmed value of some settling cue is encountered. The present study suggests instead that animals experiencing poor or degraded habitat will become less selective, and more likely to settle in poor-quality habitat before reaching isolated patches of high-quality habitat. Alternately, they may become less willing to leave a good but saturated patch and travel long distances to find new patches. If this is the case, measures of dispersal prior to habitat loss or decline will poorly predict movement after. Two studies have shown reduced likelihood of dispersal as a consequence of habitat fragmentation. Diffendorfer et al. (1995) found a decreased proportion of dispersers in fragmented patches, although those individuals that did emigrate travelled longer distances. Wolff et al. (1997) found reduced dispersal distances in recently fragmented versus continuous patches. Even qualitative predictions of the population movement response to habitat loss or change will require study of the relative importance of fixed and flexible emigration and settling cues, and the relative importance of experience prior to and during movement.

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References

- Anders, A. D., Faaborg, J. & Thompson, F. R. 1998. Postfledging dispersal, habitat use, and home-range size of juvenile wood thrushes. *Auk*, **115**, 349–358.
- Badyaev, A. & Faust, J. D. 1996. Nest site fidelity in female wild turkey: potential causes and reproductive consequences. *Condor*, **98**, 589–594.
- Baker, M. B. 1998. Individual strategies and fitness consequences of natal dispersal in desert isopods (*Hemilepistus reaumuri*). Ph.D. thesis, University of California at Davis.
- Baker, M. B. 2004. Sex biased condition dependent dispersal in desert isopods, *Hemilepistus reaumuri*. *Journal of Insect Behavior*, **17**, 579–598.
- Baker, M. B. & Rao, S. 2004. Incremental costs and benefits shape natal dispersal; theory and an example using desert isopods, *Hemilepistus reaumuri*. *Ecology*, **85**, 1039–1051.
- Baker, M. B., Shachak, M. & Brand, S. 1998. Settling behavior of desert isopods, *Hemilepistus reaumuri*, in response to variation in soil moisture and other environmental cues. *Israel Journal of Zoology*, **44**, 345–354.
- Beletsky, L. D. & Orians, G. H. 1991. Effects of breeding experience and familiarity on site fidelity in female red-winged blackbirds. *Ecology*, **72**, 787–796.
- Boulinier, T. & Danchin, E. 1997. The use of conspecific reproductive success for breeding patch selection in territorial migratory species. *Evolutionary Ecology*, **11**, 505–517.
- Brandwine, S. & Shachak, M. 1998. Population response of *Hemilepistus reaumuri* to soil moisture patchiness. *Israel Journal of Zoology*, **44**, 369–378.
- Bried, J. & Jouventin, P. 1999. Influence of breeding success on fidelity in long-lived birds: an experimental study. *Journal of Avian Biology*, **30**, 392–398.
- Brown, C. R., Brown, M. B. & Danchin, E. 2000. Breeding habitat selection in cliff swallows, the effect of conspecific reproductive success on colony choice. *Journal of Animal Ecology*, **69**, 133–142.
- Carroll, J. E., Lamberson, R. H. & Roe, R. 1995. Sinks, sources, and spotted owls: a territorial population model with continuous mortality and discrete birth. *Mathematical Biosciences*, **129**, 169–188.
- Danchin, E., Heg, D. & Doligez, B. 2001. Public information and breeding habitat selection. In: *Dispersal* (Ed. by J. Clobert, E. Danchin, A. A. Dhondt & J. D. Nichols), pp. 243–258. New York: Oxford University Press.
- Diffendorfer, J. E., Gaines, M. S. & Holt, R. D. 1995. Habitat fragmentation and movements of 3 small mammals (*Sigmodon*, *Microtus*, and *Peromyscus*). *Ecology*, **76**, 827–839.
- Dingle, H. 1996. *Migration: the Biology of Life on the Move*. New York: Oxford University Press.
- Doliguez, B., Danchin, E., Clobert, J. & Gustafsson, L. 1999. The use of conspecific reproductive success for breeding habitat selection in a non-colonial, hole-nesting species, the collared flycatcher. *Journal of Animal Ecology*, **68**, 1193–1206.
- Doliguez, B., Danchin, E. & Clobert, J. 2002. Public information and breeding habitat selection in a wild bird population. *Science*, **297**, 1168–1170.
- Dukas, R. 1998. Evolutionary ecology of learning. In: *Cognitive Ecology: the Evolutionary Ecology of Information Processing and Decision Making* (Ed. by R. Dukas), pp. 129–174. Chicago: University of Chicago Press.
- Greenwood, P. J. 1980. Mating systems, philopatry, and dispersal in birds and mammals. *Animal Behaviour*, **28**, 1140–1162.
- Haas, C. A. 1998. Effects of prior nesting success on site fidelity and breeding dispersal: an experimental approach. *Auk*, **115**, 929–936.
- Hoffmann, G. 1985. The influence of landmarks on the systematic search behaviour of the desert isopod, *Hemilepistus reaumuri*. *Behavioral Ecology and Sociobiology*, **17**, 335–348.
- Hoffmann, G. 1989. The orientation of terrestrial isopods. *Monitore Zoologico Italiano Monographia*, **4**, 489–512.
- Johst, K. & Brandl, R. 1997. The effect of dispersal on local population dynamics. *Ecological Modelling*, **104**, 87–101.
- Kareiva, P. & Wennergren, U. 1995. Connecting landscape patterns to ecosystem and population processes. *Nature*, **373**, 299–302.
- Linsenmair, K. E. 1984. Comparative studies on the social behaviour of the desert isopod *Hemilepistus reaumuri* and of a *Porcellio* species. *Symposium of the Zoological Society of London*, **53**, 423–453.
- MacNamara, J. M. 1985. Optimal foraging and learning. *Journal of Theoretical Biology*, **117**, 231–249.
- MacNamara, J. M. & Houston, A. I. 1987. Memory and the efficient use of information. *Journal of Theoretical Biology*, **125**, 385–395.
- Mangel, M. 1990. Dynamic information in uncertain and changing worlds. *Journal of Theoretical Biology*, **146**, 317–332.
- Mangel, M. 1993. Motivation, learning, and motivated learning. In: *Insect Learning: Ecological and Evolutionary Perspectives* (Ed. by D. R. Papaj & A. C. Lewis), pp. 158–174. New York: Chapman & Hall.
- Mangel, M. & Clark, C. W. 1988. *Dynamic Modeling in Behavioral Ecology*. Princeton, New Jersey: Princeton University Press.
- Mark, G. A. 1982. Induced oviposition preference, periodic environments and demographic cycles in the bruchid beetle *Callosobruchus maculatus*. *Entomologia Experimentalis et Applicata*, **32**, 155–160.
- Menzel, R., Greggers, U. & Hammer, M. 1993. Functional organization of appetitive learning and memory in a generalist pollinator, the honey bee. In: *Insect Learning: Ecological and Evolutionary Perspectives* (Ed. by D. R. Papaj & A. C. Lewis), pp. 79–125. New York: Chapman & Hall.
- Noon, B. R. & McKelvey, K. S. 1996. Management of the spotted owl: a case history in conservation biology. *Annual Review of Ecology and Systematics*, **27**, 135–162.
- Ollason, J. G. 1980. Learning to forage—optimally? *Theoretical Population Biology*, **18**, 44–56.
- Papaj, D. R. 1986. Conditioning of leaf shape discrimination by chemical cues in the butterfly, *Battus philenor*. *Animal Behaviour*, **34**, 1281–1288.
- Papaj, D. R. & Prokopy, R. 1989. Ecological and evolutionary aspects of learning in phytophagous insects. *Annual Review of Entomology*, **34**, 315–350.

- Paradis, E., Baillie, S. R., Sutherland, W. J. & Gregory, R. D. 1998. Patterns of natal and breeding dispersal in birds. *Journal of Animal Ecology*, **67**, 518–536.
- Prokopy, R. J., Cooley, S. S. & Opp, S. B. 1989. Prior experience influences fruit residence of male apple maggot flies. *Journal Insect Behavior*, **2**, 39–48.
- Pyle, P., Sydeman, W. J. & Hester, M. 2001. Effects of age, breeding experience, mate fidelity and site fidelity on breeding performance in a declining population of Cassin's auklets. *Journal of Animal Ecology*, **70**, 1088–1097.
- Reed, J. M., Boulonier, T., Danchin, E. & Oring, L. W. 1999. Informed dispersal: prospecting by birds for breeding sites. *Current Ornithology*, **15**, 189–259.
- Roitberg, B. D., Reid, M. L. & Li, C. 1993. Choosing hosts and mates: the value of learning. In: *Insect Learning: Ecological and Evolutionary Perspectives* (Ed. by D. R. Papaj & A. C. Lewis), pp. 174–194. New York: Chapman & Hall.
- Ruckelshaus, M., Hartway, C. & Kareiva, P. 1997. Assessing the data requirements of spatially explicit dispersal models. *Conservation Biology*, **11**, 1298–1306.
- Schjørring, S. 2002. The evolution of informed natal dispersal: inherent vs. acquired information. *Evolutionary Ecology Research*, **4**, 227–238.
- Shachak, M. 1980. Feeding, energy flow and soil turnover in the desert isopod, *Hemilepistus reaumuri*. *Oecologia*, **24**, 57–69.
- Shachak, M. & Brand, S. 1988. Relationship among settling, demography, and habitat selection: an approach and a case study. *Oecologia*, **76**, 620–626.
- Shachak, M. & Brand, S. 1991. Relationship among spatiotemporal heterogeneity, population abundance and variability in a desert. In: *Ecological Studies Series 86: Ecological Heterogeneity* (Ed. by J. Kolasa & S. T. A. Pickett), pp. 202–223. New York: Springer-Verlag.
- Shutler, D. & Weatherhead, P. J. 1994. Movement patterns and territory acquisition by male red-winged blackbirds. *Canadian Journal of Zoology*, **72**, 712–720.
- Stamps, J. A. & Krishnan, V. V. 1999. A learning-based model of territory establishment. *Quarterly Review of Biology*, **74**, 291–318.
- Stephens, D. W. 1987. On economically tracking a variable environment. *Theoretical Population Biology*, **32**, 1–25.
- Stephens, D. W. 1989. Variance and the value of information. *Behavioral Ecology*, **134**, 128–140.
- Stephens, D. W. 1993. Learning and behavioral ecology: incomplete information and environmental predictability. In: *Insect Learning: Ecological and Evolutionary Perspectives* (Ed. by D. R. Papaj & A. C. Lewis), pp. 195–218. New York: Chapman & Hall.
- Tella, J. L., Forero, M. G. & Donazar, J. A. 2001. Factors affecting breeding dispersal in the facultatively colonial lesser kestrel: individual experience vs. conspecific cues. *Journal of Animal Ecology*, **70**, 568–578.
- Turlings, T. C. J., Wackers, F. L., Vet, L. E. M., Lewis, W. J. & Tumlinson, J. H. 1993. Learning of host-finding cues by hymenopterous parasitoids. In: *Insect Learning: Ecological and Evolutionary Perspectives* (Ed. by A. C. Lewis & D. R. Papaj), pp. 51–78. New York: Chapman & Hall.
- Warburg, M. R., Linsenmair, K. E. & Bercovitz, K. 1984. The effect of climate on the distribution and abundance of isopods. *Symposium of the Zoological Society of London*, **53**, 339–367.
- Ward, S. A. 1987. Optimal habitat selection in time-limited dispersers. *American Naturalist*, **129**, 568–579.
- Ward, S. A., Leather, S. R., Pickup, J. & Harrington, R. 1998. Mortality during dispersal and the cost of host-specificity in parasites: how many aphids find hosts? *Journal of Animal Ecology*, **67**, 763–773.
- Waser, P. M., Creel, S. R. & Lucas, J. R. 1994. Death and disappearance: estimating mortality risks associated with philopatry and dispersal. *Behavioral Ecology*, **5**, 135–141.
- Wolff, J. O., Schaubert, E. M. & Edge, W. D. 1997. Effects of habitat loss and fragmentation on the behavior and demography of gray-tailed voles. *Conservation Biology*, **11**, 945–956.