

## INCREMENTAL COSTS AND BENEFITS SHAPE NATAL DISPERSAL: THEORY AND EXAMPLE WITH *HEMILEPISTUS REAUMURI*

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**Abstract.** Incremental (distance-dependent) costs and benefits of dispersal have received less attention than those that are qualitative. We present a dynamic programming model of settling behavior using parameters estimated from a field study of dispersal in desert isopods, *Hemilepistus reaumuri*, which walk up to thousands of meters before settling in new or already-established burrows each spring. The model shows that incremental costs of dispersal lead to right-skewed population dispersal patterns, in contrast to cost-free systems or those with unitary costs (i.e., a one-time cost of leaving a group or patch). In the model, continuous variation in habitat quality, as opposed to discrete suitable vs. unsuitable sites, allows for trade-offs with dispersal costs that lead to shifts in the likelihood of settling in a patch of a given quality. Thus, measurement of quantitative costs and benefits of movement are needed to understand population dispersal distributions. These costs or benefits may be observable during or after movement, and we examined both pre- and postsettling incremental consequences of dispersal. The daily mortality rate of traveling isopods was 4.2% during the dispersal season, higher than that of settled individuals. Successful settlers traveled more slowly, but burrows started in midseason were most likely to succeed. More distant burrows failed more often, suggesting either an additional cost of movement or a difference in the quality of individuals traveling different distances. The predicted mean dispersal duration from the simulations matched observed values closely, but was based on an unrealistic assumption of perfect knowledge of habitat quality, suggesting some other factor favors longer times before settling. Reproductive success was much higher in re-used burrows than in new burrows, making them a possible incentive for long-distance movements.

**Key words:** *behavior; condition; Crustacea; dispersal; Hemilepistus reaumuri; movement; prospecting; settling; terrestrial isopod.*

### INTRODUCTION

Dispersal can have profound effects on the persistence and genetic structure of populations and the speed that favorable mutations, invading species, or parasites can spread (Kareiva and Wennergren 1995, Dingle 1996). Theory generally predicts that the survival of dispersing individuals, relative to those that do not disperse, will shape the degree and extent of movement (Johnson and Gaines 1990, Gandon and Michalakis 2001), and this relationship has been shown qualitatively. For example, populations of baboons with higher predation pressure show higher male philopatry than those with fewer predators (Alberts and Altmann 1995). Very few studies provide empirical estimates of the quantitative costs or benefits of dispersal, particularly mortality (Johnson and Gaines 1990, Waser et al. 1994, Plissner and Gowaty 1996; but see Small et al. 1993, Van Vuren and Armitage 1994, Alberts and

Altmann 1995). Comparisons of recapture rates of individuals that are more dispersive or philopatric have been used to infer a mortality cost of dispersal (Getz et al. 1994; others reviewed in Waser and Jones [1983] and Johnson and Gaines [1990]), although it may be difficult to distinguish whether disappearing individuals dispersed or died (Clobert 1995). Comparisons of numbers of immigrants vs. emigrants (Waser et al. 1994) or numbers settled vs. unsettled at different seasons (Ward et al. 1998) have been used to indirectly infer the mortality of dispersers before settling. Tracking individuals during dispersal has yielded undetectable mortality of dispersing individuals relative to those that remain sedentary in two species (Small et al. 1993, Gillis and Krebs 2000), but a range of increased mortality has been observed in others, from 16% greater in marmots (Van Vuren and Armitage 1994) to 2–10 times greater in baboons (Alberts and Altmann 1995), and twice the mortality in Red-cockaded Woodpeckers (Daniels and Walters 2000). None of these studies shows how increased distances traveled might increase costs. Lack of data on incremental consequences of movement might have shaped the devel-

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opment of theories used to understand population dispersal distributions.

Several earlier models have examined how a cost of dispersal can be balanced by competition and habitat variability to generate evolutionarily stable rates of emigration from a single patch or between a pair of patches (Hamilton and May 1977, Comins et al. 1980, Hastings 1983, McPeck and Holt 1992). General predictions from these models include that survival costs are critical in determining proportions of dispersers, that some dispersers will be favored even at very high costs of dispersal, and that spatial heterogeneity will dominate temporal heterogeneity in favoring dispersal. At the same time, simulation models have been developed to see if observed population dispersal distance distributions can be accounted for by extremely simple settling dynamics, including competition for a limited number of suitable sites (Murray 1967, Waser 1985, Tonkyn and Plissner 1991, McCarthy 1997, 1999) or constant rates of stopping (Buechner 1987, Caley 1991). In these models, individual behavior is affected neither by mortality costs nor by variation in habitat quality. In cases where dispersing individuals experienced mortality (Buechner 1987, McCarthy 1999), settling decisions were not affected by that cost. The question still remains whether individuals disperse only far enough to settle in the first available territory, or if the definition of an available territory varies with both incremental costs and benefits of dispersal, as well as continuous variation in habitat quality. Only recently have models examined how incremental costs of dispersal influence dispersal distance distributions (Rousset and Gandon 2002). Just as importantly, empirical measures of variation in mortality and reproductive success as a function of distance are needed to justify consideration of their effects on dispersal patterns.

While mortality is observable during movement, some consequences of dispersal are only observable after settling. Increased dispersal might affect individual condition, timing of settling or breeding, and habitat quality or familiarity. These mechanisms should lead to observable relationships between dispersal distance and future survival or fecundity. Studies of natal dispersal in birds have observed either no effect (Plissner and Gowaty 1996), an increase (Spear et al. 1998), or a decrease (Pärt 1990) in future female fecundity. Among males, increased dispersal distances were associated with reduced (Pärt 1990) or enhanced survival (Spear et al. 1998). Among fledglings, Greenwood et al. (1979) found increased return rates for those with more dispersive mothers. Since dispersal can have multiple interacting effects during and after the act of movement, studies are needed to examine each of these potential consequences. Costs observable only during dispersal might be balanced by benefits observable only after dispersal, or the reverse pattern might become evident.

We used a dynamic programming model (Mangel and Clark 1988) of natal dispersal to examine the effects of incremental mortality during dispersal and continuous variation in habitat quality on settling behavior and population dispersal distributions. Dynamic programming is useful for optimizing time-limited foraging strategies, such as those faced by an unsettled individual in a limited dispersal season. The optimal strategies defined by the model were then used to simulate populations of dispersers as they encounter habitat patches drawn from the same distributions used by the dynamic model. The model is general, but is based on the biology of the desert isopod *Hemilepistus reaumuri*. We present the results of the field study used to measure parameters in the model and generally evaluate several potential costs and benefits of increased time or distance traveled in desert isopods. This species was chosen because its small size, short life-span, terrestrial life style, and intense dispersal season make it well suited to measuring multiple fitness consequences of dispersal.

We examined effects of distance or time spent moving on survival, both before and after settling, and on physiological condition during movement. We used mark-recapture analysis on individuals traveling in an enclosed corridor to measure daily survival of traveling isopods. Dispersal could be a physiologically draining stage, during which individuals search for superior sites to settle at some cost to their own health. Conversely, it could serve to grow or feed prior to breeding. We measured changes in condition as a function of time spent traveling and distance traveled. We examined two potential consequences of movement on reproductive success, measured as survival of the family until the following autumn: (1) effects of time of burrow establishment, and (2) effects of the amount of time spent traveling before settling. The two are undoubtedly related, yet they are not the same. If only the first effect were present, perhaps due to seasonal habitat decline or competition for limited habitat, prolonged dispersal would be costly later but not earlier in the season. The second effect might reflect changes in body condition and/or refinement of habitat selection. In cavity-nesting or burrowing species, such as desert isopods, a previously established and successful site may be a rare, valuable resource for dispersers. We compared the probability of successful reproduction in newly initiated vs. reused burrows, to see if they might represent a valuable resource that might justify longer distance movements or long times spent before settling.

## METHODS

### *The model*

The model solves for the optimal decision of whether to settle or continue searching, as a function of time in the season and habitat quality. Any optimization model has four components (Oster and Wilson 1978):

(1) a state space, (2) a strategy set, (3) an optimization criterion, and (4) a set of constraints. The state space in this model is the quality of the site an individual currently occupies, in terms of the likelihood of reproducing successfully in that site, as most variation in fitness is accounted for by family survival (Shachak and Brand 1988). The mean and variance in habitat quality were taken from the open-field study (see *Experiments*), arcsine-transformed so that habitat quality could be normally distributed, with 40 levels for the state variable to approximate a normal distribution of site quality. Although levels are used to approximate continuously varying habitat, the cutoff of habitat quality separating settling vs. searching is similar to the two patches in choice models such as Ward (1987). The cutoff in this and other models is a measure of habitat selectivity, and given an unchanging but continuous distribution of habitat quality, a decrease in selectivity (the cutoff) would lead to an increase in individuals' probability of settling in that habitat.

The strategy set consists of choosing whether to settle in the current site or leave the site to continue searching. The optimization criterion is the probability of successful reproduction, which is the product of survival to the end of the dispersal season and the probability that the burrow survives until the following dispersal season. The constraints are the distribution of site qualities, as well as the duration of the dispersal season and the mortality associated with searching or settling. The search unit is one day, which corresponds to ~15 m traveled for desert isopods (Baker 1998). Distance and time are used interchangeably as search units when discussing model results. The season lasts 40 days, the approximate length of the isopod dispersal season. In versions of the model with an incremental mortality cost of dispersal, individuals have a probability of mortality of 0.042 per search unit when searching, and a probability of mortality of 0.025 when settled. This value reflects a maximum settled-mortality estimate, to minimize the observed cost of dispersal and observe its effect in the model. In versions of the model without an incremental cost, both settled and unsettled individuals have a daily mortality of 0.025.

Expressed formally, the terminal fitness function is

$$F(x, T, T) = P_{\text{rep}}(x) \quad (1)$$

which states that the fitness  $F$  at the final time period ( $T$ ) is equal to the probability of successful reproduction ( $P_{\text{rep}}$ ), which is a function of the quality of the occupied site  $x$ . At any given time period prior to  $T$ ,

$$F(x_i, t, T) = \max[F_{\text{search}}(t, T), F_{\text{settle}}(x_i, t, T)] \quad (2)$$

where  $x_i$  is the quality of the currently occupied site ( $i$ ), and  $i$  can take any of 40 levels in quantitative versions or two levels in qualitative versions,  $t$  is the current search unit (1 day),  $T$  is the time horizon (40 d), and  $F_{\text{search}}$  and  $F_{\text{settle}}$  are fitness functions for searching or settling, respectively, dependent on the parameters

in parentheses. The fitness for individuals searching for a new site as a function of time during the season is

$$F_{\text{search}}(t, T) = (1 - \beta_{\text{search}}) \left[ \sum_{i=1}^{40 \text{ or } 2} \lambda_i F(x_i, t + 1, T) \right] \quad (3)$$

where  $\beta_{\text{search}}$  is the mortality of searching isopods, and  $\lambda_i$  is the probability of encountering a site of quality  $i$  when searching. The fitness for individuals settling in the currently occupied site as a function of site quality and time during the season is

$$F_{\text{settle}}(x_i, t, T) = (1 - \beta_{\text{settle}})^{(T-t)} F(x_i, T, T) \quad (4)$$

where  $\beta_{\text{settle}}$  is the mortality of settled individuals. The dynamic model is solved iteratively starting from  $t = T$  and cycling backwards, solving for the optimal strategy and expected fitness. The dynamic model provides the strategies used by individuals in simulated populations dispersing in different years.

The simulations addressed two general questions: (1) How do incremental costs of movement, and (2) how does discrete vs. continuously varying habitat quality shape population dispersal distributions? We used the dynamic model to simulate populations dispersing in years with different distributions of habitat quality and with or without an incremental cost of movement. We selected each individual year's mean and variability of habitat quality from the among-years' normal distributions of mean ( $N(\theta_0 = 0.43, \phi_0^{1/2} = 0.09)$ ) and 1 SD ( $N(E_{(\phi)} = 0.12, \phi_{(\phi)}^{1/2} = 0.015)$ ) in habitat quality (the arcsine-transformed probability of successful reproduction after settling). The means of habitat parameters were taken from the two years for which we had data, but the variance distribution had to be chosen arbitrarily. In versions with qualitative variation in habitat, search sites were given a 0 or 1 probability of successful reproduction in proportion to the overall continuous mean probability of reproductive success.

We simulated populations of 500 individuals using the optimal strategies calculated by the model to make settling decisions dispersing in 50 different seasons. Each individual within a population experienced a sequence of sites drawn from that year's distribution until it died or chose to settle. Its decision to settle was made using the dynamic programming model thresholds for that year's distribution of sites. Daily cutoff values of habitat quality favoring settling, daily probabilities of settling, and population dispersal distributions were saved.

## EXPERIMENTS

### *Species and study area*

*Hemilepistus reaumuri* (see Plate 1) is a monogamous, semelparous isopod found in deserts in North Africa and Central Asia in areas receiving 50–400 mm annual rainfall (Coenen-Stass 1984; M. B. Baker, *personal observation*). From February until early March, nine-month-old young from the previous year emerge



PLATE 1. An adult isopod (*Hemilepistus reaumuri*) investigates the entrance of an occupied burrow during the dispersal season. Photo credit: Mitchell Baker.

from their natal burrows and search either for sites suitable for establishing new burrows or for burrows already established. Isopods initially walk in random directions, but maintain a linear trajectory once a course is established (Hoffman 1989). In one study, individuals most commonly traveled 250–450 m before settling (Warburg et al. 1984). In another, the mean distance traveled was 171 m, with a median distance of 71 m and a maximum observed distance moved of 1100 m (Baker 1998). Desert isopods can start burrows themselves, or join already established burrows, so they are not limited to a fixed set of vacant territories (Linsenmair 1971). Successful dispersal in the spring culminates in occupation of a burrow by a mated pair that can be censused for family survival the following autumn. Females typically start new burrows, with males competing for access to females, though males sometimes dig their own burrows, more frequently later in the season (Linsenmair 1984, Baker 1998). A more complete description of *H. reaumuri*'s life cycle can be found in Shachak (1980), and Linsenmair (1971, 1984).

The study site was located on a loess plain (Sde Zin), in the central Negev, Israel (34°46' E, 30°50' N), 500 m above sea level, with mean annual rainfall of 104 mm (ranging from 34 to 167 mm over the last 30 years). The area is covered by thick loessal serozem soil. Perennial vegetation cover is 10–15%, composed of *Hamada scoparia*, *Artemisia herba alba*, and *Reaumuria palestina* shrubs. The study site has been fenced for 26 years.

#### *Family survival of free-ranging isopods*

Family survival of old and new burrows was measured on 25, 5 × 10 m (1996) or 10 × 10 m (1997) open-field plots, spaced regularly on a 4 × 10<sup>4</sup> m<sup>2</sup> grid on the Zin plain. Survival was used to estimate variation in habitat quality for use in the model, and also

to evaluate whether previously successful burrows might serve as a rare, valuable resource for settlers. We marked all burrows in the spring with an aluminum tag, 5 cm to the south of each burrow entrance. Burrows were classified in two categories: old burrows were those in which a family had successfully been raised the previous season, and new burrows were initiated in the current season. We assessed burrow age by examining the feces surrounding the burrow Baker (1998). Family survival was determined the following October by either observing a guard at the burrow entrance or observing the fecal mound surrounding the burrow. We used the presence of all size classes of feces to infer family survival (Shachak and Brand 1988). To examine old vs. new burrow survival, we also included new and old burrows censused in a 300 × 3 m enclosed corridor. Old- vs. new-burrow survival in each year was analyzed using  $\chi^2$  tests. The mean and variance of family survival among open plots provided the habitat variability parameters in the model.

#### *Corridor experiments*

A corridor with dimensions 300 m long by 3 m wide was erected on the Zin Plain to measure the incremental mortality cost of dispersal used in the model, as well as to estimate other potential incremental costs and benefits of increased movement before settling, in terms of body condition, time of settling, and time or distance traveled before settling.

*General procedures.*—The corridor was created using strips of corrugated plastic sheeting, 30 cm in width, to form a continuous wall that extended 15–20 cm above ground. In the two seasons of the study, we collected isopods from their burrows at emergence and brought them indoors to be weighed, measured (length and width), and marked using model paint. We held the isopods overnight in cages above a saturated K<sub>2</sub>SO<sub>4</sub> solution to maintain humidity at or above 95% at room temperature (Winston and Bates 1960), corresponding to humidity within isopod burrows (Coenen-Stass 1989). Body condition was calculated using a residual index (Jakob et al. 1996), as the residual of the regression of log-transformed mass on log-transformed length and width. Thus, condition was independent of length or width.

We released the marked isopods at the ends of the corridor the day following capture at the start of the daily active period. In 1996, isopods were collected using drift fences and collecting traps placed every 25 m in the corridor. The collecting traps were continuously monitored during the daily active period. Marked isopods were recorded and immediately replaced in the next segment of the corridor to allow them to continue movement. In 1997, movement of individuals in the corridor was not hampered. Individuals were observed either through short censuses of the entire corridor, where an observer traveling from one end to the other would stop every five meters and record each visible

marked isopod for 50 s, or during the course of the continuing surveys of isopod burrows in the corridor. Marked isopods reaching an end of the corridor were reintroduced at the opposite end, exposing them to habitat they may have encountered, but less recently and without changing directions, as would be the case if they were reversed in the corridor.

In 1997, we conducted seven censuses of newly initiated burrows and of old burrows in the dispersal corridor continuously over 55 days. New and old burrows were marked as in the open plots. New burrows contain either an individual or a mated pair and are shallow enough that one or both occupants can be removed unharmed with a bent wire, identified, and replaced. If the top isopod could not be removed, or if there was only a single individual, the burrow was rechecked in later surveys. Old burrows were not accessible enough to census for all marked settlers, but any observed marked settlers were recorded. In October, burrows were censused for family survival.

*Daily mortality of unsettled isopods.*—Recaptures of individuals in the study corridor in 1997 were used to estimate survival of settled and unsettled isopods during dispersal, whose values were used in the dynamic programming model. A total of 1349 marked isopods were released into the corridor; 654 were female, and 631 were classified as of high condition, defined as having a positive residual index (sexes pooled, condition fit separately for each sex). Survival and recapture probabilities were estimated using the program SURGE to fit a Cormack-Jolly-Seber model (Lebreton et al. 1992) to the recapture data. Three SURGE models were tested for all adults pooled: (model A) both survival and recapture probability vary with time, (model B) only recapture probability varies, and (model C) neither survival nor recapture varies.

Survival of male and female, below- or above-average (corrected for sex) mass, and below- or above-average condition were tested for significant differences. Models were selected to maximize explanatory power and minimize parameters, using the likelihood ratio statistic (LRS; Lebreton et al. 1992, Cooch et al. 1996).

Observed settlers were recorded as recaptured and removed from the analysis on the date of discovery in a burrow. The SURGE program was designed for analysis of year-to-year survival, and as such is limited to 21 capture/recapture occasions. The dispersal season lasted 63 days in 1997. In order to use the program, three days were pooled into each recapture occasion for SURGE. All comparisons and statistics were performed on the pooled recapture occasions, but the estimates of daily survival or recapture rate are actually the cube roots of the estimates per recapture occasion.

*Changes in body condition during movement.*—We measured changes in body condition during the dispersal season in 1996 as a potential incremental cost of dispersal above direct mortality. There were three

treatments after isopods were collected at emergence: one that examined mass, body moisture, and organic matter at emergence; one that looked only at body mass during travel; and one that measured mass, body moisture, and organic matter once during travel.

To analyze body condition at emergence, 257 isopods collected from 25 burrows isopods were weighed immediately after collection and their lengths and widths measured. They were then sacrificed by freezing and dried to a constant mass over three days at 60°C to determine fractional water content. To determine dry organic matter content, 138 of the 257 already-dehydrated isopods were placed in an ashing oven at 800°C for two hours, and then reweighed.

To repeatedly measure changes in mass during dispersal, a second group of 99 isopods were collected at varying distances of 25–225 m from the end of the dispersal corridor, weighed, and immediately replaced in the corridor at the point of removal. Individuals were recaptured up to four times, resulting in 155 measurements from the 99 individuals. Change in mass as a function of the distance dispersed and time in the corridor was calculated using linear or quadratic regression.

To examine organic matter content and water content and loss in traveling isopods, a third group of 58 individuals was collected once as they traveled in the corridor at distances ranging from 25 to 300 m. These were weighed, dehydrated, and weighed, ashed, and weighed once more in the same manner as those collected at emergence. Body moisture was regressed against time and distance dispersed. Body moisture can only be measured once gravimetrically in any individual, so we estimated water loss in traveling isopods by comparing water content at recapture with that predicted by the regression of water content on mass at emergence in the first group. We estimated the percentage body mass lost per hour as follows:

$$\left[ \frac{\left( \frac{H_2O_{\text{recap}} - H_2O_{\text{emergence}}}{\text{mass}_{\text{emergence}}} \right)}{(\text{days to recapture}) \times 24} \right] \times 100$$

where  $H_2O_{\text{recap}}$  is the fractional water content of recaptured isopods multiplied by body mass at recapture, and  $H_2O_{\text{emergence}}$  is the estimated fractional water content of emergers multiplied by body mass at emergence. We examined rates of water loss as a function of distance, duration, and speed of movement.

*Consequences of distance traveled, time of settling and duration of movement.*—Linear and quadratic effects of distance on burrow survival were analyzed using regression. Because it was possible for individual isopods to reach an end of the corridor and reverse direction before being observed, only those marked settlers with multiple recaptures that allowed inference of the direction of movement were used to examine

new burrow success as a function of distance traveled. Of 211 burrows occupied by marked isopods, 71 were of known distance traveled before settling.

We approximated the timing of burrow initiation from the seven continuously operating censuses of isopod settling conducted in 1997. While a mean value of seven days elapsed between censuses at a given location in the corridor, some censuses were carried out in as few as five days. The day that a burrow was first identified, pooled into five-day groups, was used as a rough estimate for when the burrow was initiated. This analysis included all burrows in the corridor started by marked or unmarked individuals ( $N = 1932$ ). The arcsine-transformed proportion of successful burrows for each five-day period was analyzed using weighted polynomial regression as a function of approximate initiation date.

The subset of burrows that were settled and still occupied at the end of the seasons by marked individuals ( $N = 116$ ) were analyzed for survival through the fall as a function of time before settling. We analyzed the relationship as a survival problem, with time until settling instead of time to failure or death as the independent variable. We tested the difference in survival functions generated by the Kaplan–Meier method using both log-rank and Wilcoxon  $\chi^2$  tests, because of their emphases on later (log-rank) vs. earlier (Wilcoxon) settling times (Kalbfleisch and Prentice 1980).

## RESULTS

### *The model*

A mortality cost of dispersal, (higher mortality prior to settling) increases the probability of settling (reduces selectivity) and leads to shorter mean dispersal and more right-skewed population dispersal distributions (Fig. 1A). Time to settle with a mortality cost of dispersal was  $7.1 \pm 6.4$  search units (mean  $\pm 1$  SD), compared to  $14.2 \pm 10.3$  search units with no increased mortality prior to settling. Toward the end of the season, all individuals become more likely to settle (the site quality cutoff is lower, reflecting low selectivity), but early in the season, the presence of a mortality cost greatly lowers the threshold for settling relative to the no-cost situation. However, mortality costs only influence dispersal behavior if there is continuous variation in habitat quality. If habitat varies categorically into suitable and unsuitable sites, selectivity and the probability of settling no longer changes with time during the season, nor is the probability of settling affected by increased mortality during movement (Fig. 1B). The slightly higher frequency of longer dispersal distances without a mortality cost is due to the survival of a greater number of unsettled individuals, not due to different behavior. Reduced continuous variation in habitat quality reduces early selectivity and population mean dispersal distance. If habitat variability was halved from observed levels (mean of 1 SD of arcsine-

transformed family survival equals 0.06 vs. 0.12) with the observed mortality cost of dispersal, the mean distance before settling declined to  $6.0 \pm 5.3$  search units (mean  $\pm 1$  SD).

### *Experiments*

*Family survival of free-ranging isopods.*—The success of occupants of old burrows from the previous season vs. occupants in new burrows in the open census plots in 1996 and 1997, and in the dispersal corridor in 1997, are presented in Table 1. Family survival was higher and appeared to be less variable among years in old vs. new burrows. Mean breeding success in old burrows ranged from 26.5 to 29.3% in the different treatments and years. Mean breeding success in new burrows ranged from 10.5 to 17.8% in the different treatments and years. In addition to providing the distribution of habitat quality in the model, the 1997 mean percentage of open-field survival (17.8%) was prorated over the six-month period between spring and fall censuses to estimate the mortality of settled isopods.

#### *Corridor experiments.*—

1. *Daily mortality of unsettled isopods.*—Both SURGE models with variable recapture rates were significantly better than the models without (model A vs. model C (see *Experiments: Corridor Experiments: Daily mortality of unsettled isopods*), LRS = 717.792, df = 36,  $P < 0.001$ ; model B vs. model C, LRS = 690.219, df = 19,  $P < 0.001$ ). The model with constant survival rates but variable recapture was insignificantly worse than the model where both survival and recapture rates varied (model A vs. model B, LRS = 27.573, df = 17,  $P < 0.06$ ). The estimated survival rate for encounter occasions was 0.868, with a 95% CI range of 0.845–0.888. This translates into a daily survival rate of 0.958, which was the value used in the model. The recapture rate estimates from model B are presented in Appendix A, and graphed in Fig. 2. We fit two curves to the recapture rate estimates, one that omits the final time period, and one that includes all the data. The justification for omitting the final time period is that all 69 recaptures during the final time period were of settled isopods, rather than traveling isopods. With the final time period omitted, there is a significant quadratic relationship between recapture probability and time during the season, indicating a peak in the ability to find marked isopods in the middle of the dispersal season. The variable survival rates from model A are presented in Appendix B.

There was no linear ( $R^2 = 0.100$ ,  $P = 0.18$ ) or quadratic ( $R^2 = 0.144$ ,  $P = 0.29$ ) relationship between time and survival (see Appendix B). Survival rates were almost identical for individuals of above- or below-average body mass or condition (assuming equal recapture rates that varied with time). Survival rates for males were significantly higher than females (male survival, 0.885, 95% CI, 0.856–0.908; female survival, 0.855, 95% CI, 0.828–0.878). The LRS for models with

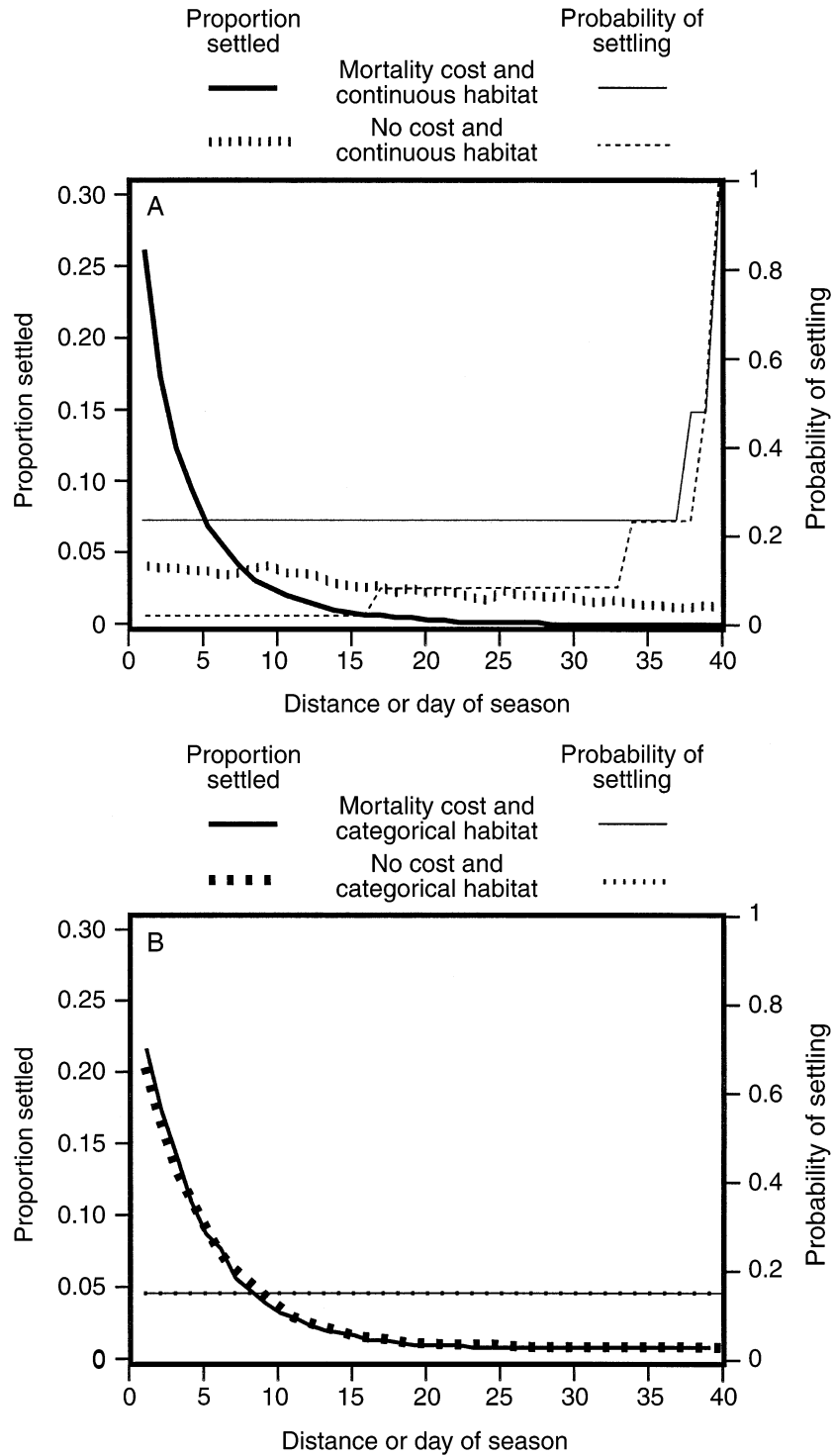


FIG. 1. (A) Simulated population dispersal distributions (thick curves) and probabilities of settling (thin curves), with or without an incremental mortality cost of dispersal (solid and dashed lines, respectively), when habitat quality varies continuously. (B) Simulated population dispersal distributions (thick curves) and probabilities of settling (thin curves), with or without an incremental mortality cost of dispersal (solid and dashed lines, respectively), when there are two categories of habitat quality with fitness values of 1 or 0.

TABLE 1. Success of new burrows vs. old burrows from the previous season. The three analyses are on data sets from open  $5 \times 10$  m or  $10 \times 10$  m census plots in 1996 and 1997, and from the dispersal corridor in 1997.

Burrow type	No. successful (percentage successful)	No. unsuccessful (percentage unsuccessful)	Total no. isopods
1996 open plots ( $\chi^2(L-R) = 101.803, P < 0.0001$ )			
New	180 (10.5)	1537 (89.5)	1717
Old	218 (26.5)	849 (72.6)	822
Total	398 (15.7)	2141 (84.3)	2539
1997 open plots ( $\chi^2(L-R) = 38.425, P < 0.0001$ )			
New	332 (17.8)	1534 (82.2)	1866
Old	320 (27.4)	849 (72.6)	1169
Total	652 (21.5)	2383 (78.5)	3035
1997 corridor ( $\chi^2(L-R) = 77.644, P < 0.0001$ )			
New	245 (12.7)	1691 (87.3)	1936
Old	161 (29.3)	389 (70.7)	550
Total	406 (16.3)	2080 (83.7)	2486

Note: The table reports results from log-rank (L-R)  $\chi^2$  tests.

the same variable recapture rate for males and females but different invariable survival rates was significant (LRS = 4.817, df = 1,  $P < 0.03$ ). This translates into a daily survival rate of 0.963 for males vs. 0.953 for females.

2. *Changes in body condition during movement.*—Traveling isopods weighed less, had lower body moisture, and had a higher proportion of organic matter than emerging isopods (Table 2). Despite the significant difference in organic matter of traveling and emerging isopods, there is no relationship between distance traveled ( $R^2 = 0.021, P = 0.30, N = 57$ ) or time spent moving ( $R^2 = 0.001, P = 0.87, N = 57$ ) and the fraction of dry matter composed of organic matter. Neither was there a relationship between distance traveled ( $R^2 < 0.001, P = 0.96, N = 57$ ) or time spent moving ( $R^2 < 0.001, P = 0.87, N = 57$ ) and the amount of organic matter (using linear regression). In contrast, body mass (Fig. 3) declined with both time and distance dispersed. Fractional water content also declined significantly with distance ( $R^2 = 0.10, P < 0.02$ ) and with time ( $R^2 = 0.12, P < 0.008$ ) dispersed ( $N = 55$ ).

The relationship between estimated rate of water loss and distance traveled was not significant, although the relationship was positive, suggesting a trend toward slower weight loss in more distant recaptures (per-

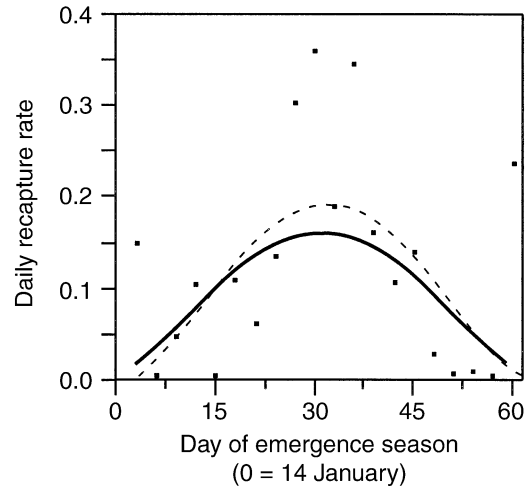


FIG. 2. Capture rates are highest in the middle of the season, as seen from the estimated daily recapture probabilities from a model using SURGE with variable recapture rates and a constant survival rate (Model B). The fitted curves are of the arcsine-transformed recapture rates. The solid curve is fitted to all points and is not significant ( $R^2 = 0.215, P = 0.128$ ). The dashed curve is fitted to all but the last recapture estimate ( $R^2 = 0.475, \sin^{-1}[(\text{recap})^{1/2}] = 0.0988[(\text{no. days})/3] - 0.00514[(\text{no. days})/3]^2 - 0.0246; P = 0.0058$ ).

centage change per hour =  $-0.0807 + 0.00021[\log(\text{no. meters per day})]$ ,  $N = 55, R^2 = 0.06, P < 0.075$ ). The estimated rate of water loss of traveling isopods as a function of duration of dispersal is presented in Fig. 4a. The log-transformed regression fits well, but the pattern appears to be one of high variability at shorter times, with an asymptotic value of  $\sim 0.036\%/h$  in the longer distance recaptures. Individuals that moved more rapidly through the corridor had higher water loss rates (Fig. 4b).

3. *Consequences of distance traveled, time of settling and duration of movement.*—Longer distances traveled before settling were associated with lower probabilities that a family survived until autumn ( $\sin^{-1}(\text{survival})^{1/2} = 0.7354 - 0.2728(\ln(\text{distance}))$ ), where distance is rounded to the nearest 5 m;  $N = 71$ , adjusted  $R^2 = 0.50, P = 0.045$ ). However, successful burrows had longer times to settling. The K–M survival curves for time until settling of isopods in successful and unsuccessful burrows (Fig. 5a) are significantly

TABLE 2. Mass, body water content, fraction of dry matter composed of organic matter, and length of emerging and traveling isopods (mean  $\pm$  1 SD).

Variable	Emergers	N	Traveling isopods	N	P
Body mass (mg)	244.7 $\pm$ 47.5	252	222.3 $\pm$ 44.2	56	0.0039
Fraction H <sub>2</sub> O	0.667 $\pm$ 0.033	252	0.636 $\pm$ 0.028	56	0.0001
Fraction organic	0.624 $\pm$ 0.057	147	0.670 $\pm$ 0.062	57	0.0001
Length (mm)	17.0 $\pm$ 1.2	229	17.0 $\pm$ 1.0	56	0.864

Notes: Length is included as a control for body size. Wilcoxon tests were performed on all variables except body length, which was normally distributed (Shapiro–Wilk test,  $W = 0.987, P < 0.76$ ).

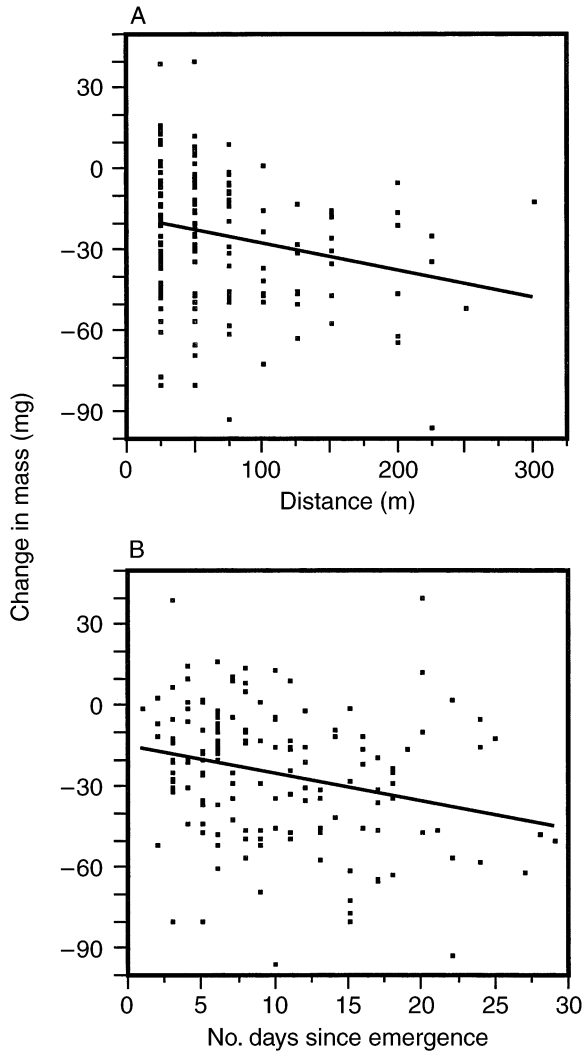


FIG. 3. Body mass declines significantly with (A) distance traveled ( $R^2 = 0.052$ ,  $P < 0.004$ ), and (B) time before recapture ( $R^2 = 0.073$ ,  $P < 0.0009$ ) ( $N = 155$ ).

different according to the Wilcoxon test ( $\chi^2_1 = 5.13$ ,  $P < 0.02$ ), and the log-rank test ( $\chi^2_1 = 3.8272$ ,  $P = 0.05$ ). Since longer distances traveled were negatively correlated with breeding success, but longer times positively correlated with breeding success, slower movement should lead to higher probabilities of new burrow success; this indeed was the case (Fig. 5b). The probability of family survival increased with time of initiation through most of the emergence and settling season, and then declined toward the end of the season (Fig. 6).

DISCUSSION

Costs of dispersal can have profound effects on habitat selectivity and population dispersal patterns. As in most dynamic programming models of foraging (Mangel and Clark 1988), selectivity (the threshold of hab-

itat quality favoring settling) declines as the end of the dispersal period approaches, thus the probability of settling increases. However, selectivity only changes if habitat varies continuously. At any given time, patches may be suitable or unsuitable, but the threshold changes as habitat variation, costs, and time vary. These relationships are not new, but the simulation results highlight how definitions of dispersal and assumptions about costs and habitat variation determine predicted individual behavior and patterns of population dispersal.

If dispersal is defined as emigration, factors operating at the natal site, such as local extinction and the

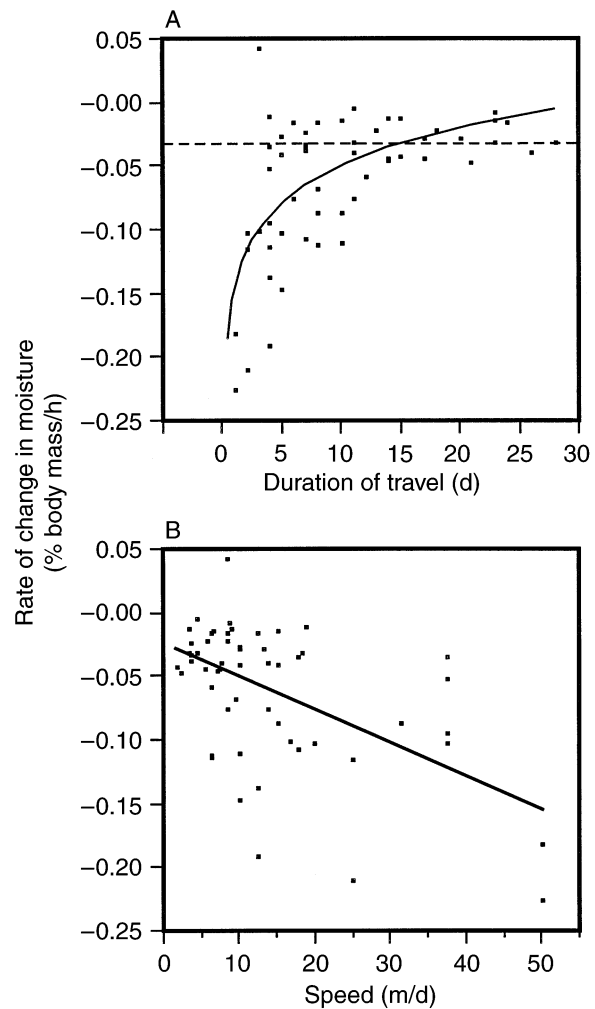


FIG. 4. Estimated rate of change of isopod body moisture as a function of duration or speed of movement. (A) The fit (solid curve) is a linear regression of change in percentage moisture on the log-transformed duration (percentage change per hour =  $-0.1489 + 0.04347[\log(\text{no. meters per day})]$ ,  $N = 55$ ,  $R^2 = 0.40$ ,  $P < 0.0001$ ). The dashed line is the mean rate of water loss of the longest (17) duration observations. (B) The fit (solid curve) is a linear regression (percentage change per hour =  $-0.0244 - 0.00256[\text{no. meters per day}]$ ;  $N = 55$ ,  $R^2 = 0.29$ ,  $P < 0.0001$ ).

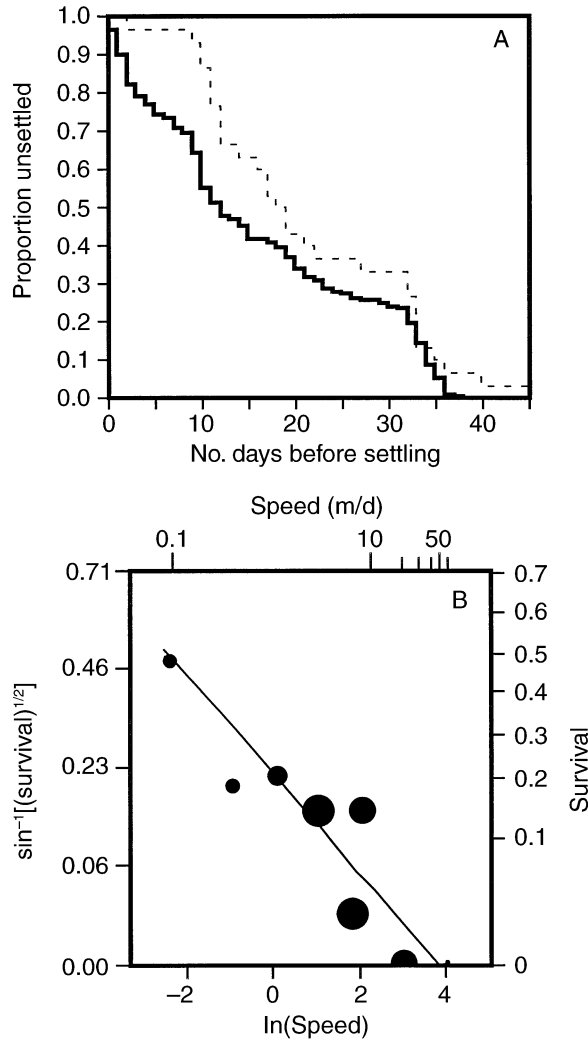


FIG. 5. Relationships among time until settling, speed of movement, and new burrow success. (A) Successful burrows were started after a longer presettling period, as shown by the product-limit survival estimates for unsettled isopods in two groups, those whose burrows succeeded (dashed line,  $N = 32$ ) and those whose burrows failed (thick line,  $N = 84$ ). (B) Faster movement before settling was associated with lower burrow survival. Data are grouped to the nearest  $\ln(\text{speed})$ , and dot size is proportional to the number of individuals in each data point. The weighted linear fit using arcsine-transformed probability of new-burrow survival fit to  $\ln(\text{distance})$  is:  $\sin^{-1}(\text{survival})^{1/2} = 0.4901 - 0.1261[\ln(\text{speed})]$  ( $N = 71$ , adjusted  $R^2 = 0.75$ ,  $P = 0.0071$ ).

risk of mating or competing with close kin, will be seen as influencing dispersal (Gandon and Michalakis 2001). However, incremental benefits such as the potential to find a slightly better site will not be considered, and, most importantly, predictions about distance distributions will not be possible. The interactions of mortality costs of searching, habitat variation, and a limited time for movement on dispersal were described by Ward's (1987) two-patch model of habitat selection. Application of foraging theory in order to adjust the

thresholds for choosing to settle will improve the predictive power and understanding of population dispersal patterns of increasingly sophisticated and spatially explicit simulation approaches. Most simulation models that generate population dispersal distance distributions do not include continuously varying habitat, nor do they allow flexible decisions that reflect how categories such as suitable or unsuitable may change depending on habitat variation and search costs. Predictions about dispersal distributions are qualitatively affected if mortality is proportional to distance or time until settling, and if habitat varies continuously.

Increased incremental mortality costs of dispersal or decreased habitat variability will lead to reduced selectivity early in the season, and a more right-skewed population dispersal distribution, even in the absence of constraints on available nesting sites or density-dependent effects on breeding success. Our model balanced one potential cost of dispersal, mortality during movement, against a potential benefit, location of superior habitat. However, habitat variation is not the only factor that can interact with costs of dispersal to generate dispersal distributions. For example, Rousset and Gandon (2002) solved for evolutionarily stable dispersal distributions in one- and two-dimensional landscapes where incremental costs of dispersal were opposed by competition among relatives, a postsettling cost. In their model, dispersal was a multilocus trait, with each locus providing a relative density at a given distance. Habitat was uniform, but avoidance of competition selected for dispersal, and their approach yielded an identical effect of incremental costs vs. a unitary cost of emigration to that of our dynamic programming model and simulation.

This study found significant mortality costs as a function of increased time spent before settling, and

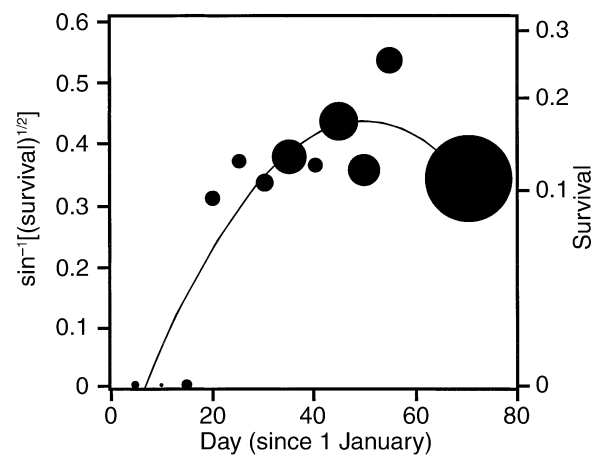


FIG. 6. New-burrow survival as a function of the day (since 1 January) of initiation. The weighted curve fit using the arcsine-transform of new-burrow survival pooled in five-day periods is:  $\sin^{-1}(\text{survival})^{1/2} = -0.1282 + 0.0223(\text{day}) - 0.00022(\text{day})^2$  ( $N = 1932$ , adjusted  $R^2 = 0.57$ ,  $P = 0.0074$ ).

reduced probability of successful reproduction with increasing distance traveled. At the same time, slower movement and increased time before settling were associated with higher probability of successful reproduction. Dispersal is a trait resistant to manipulative treatments. Without manipulation, it is impossible to distinguish a benefit of greater time spent before settling from the possibility that higher quality individuals are taking more time to settle. Indeed, if time before settling has rewards, and higher condition individuals can afford more time before settling, these two effects should be correlated.

Isopods experience high mortality during dispersal. It is not known what proportion of mortality is due to predation, and what proportion is due to factors such as starvation, illness, or exposure. A study of predation risk using tethered isopods in different habitats (Baker 1998) observed a disappearance rate of 2.4%, suggesting that predation could account for a significant fraction of observed mortality. The use of a corridor necessarily involved trade-offs of possible interference of isopods or their predators with the ability to have high recapture rates unbiased by distance (Porter and Dooley 1993, Baker et al. 1995, Koenig et al. 1996). The density of scorpions, a primary predator (Shachak 1980), was similar inside and outside the corridor (Baker 1998), and vertebrates should have had little difficulty moving over the 15–20 cm barrier.

In order for mortality to act as a cost of dispersal, the mortality rates of settled individuals must be lower than that of those that move. Although daily mortality of isopods in family burrows was not measured, the overall survival of isopod burrows in the year of the study to the end of the growing season was recorded (0.215; Table 2). In order for a family to survive to the following season, both parents must live until July (Shachak 1980). If the observed survival was distributed from the beginning of the emergence period through July and included both parents, a daily individual mortality rate of 0.005 would be indicated. (If family survival was the product of both parents surviving all 150 d of the breeding season, then daily survival =  $[0.215^{1/150}]^{1/2} = 0.995$ .) If, however, mortality is not uniform during the season, then an even distribution is not appropriate. If all the burrow mortality were concentrated in the first month after settling, before safer depths are reached by the burrowing pair (Shachak 1980, Coenen-Stass 1989), then daily mortality is 0.025 ( $[0.215^{1/30}]^{1/2} = 0.975$ ), still less than two-thirds the mortality observed in traveling isopods. The high observed cost of dispersal is consistent with indirect demographic estimates of highest population decline during the dispersal season (Shachak and Brand 1988).

Water loss may limit dispersal. The estimated rates of water loss were low compared to earlier laboratory studies (Coenen-Stass 1981, Warburg 1987), and this might reflect behavioral mechanisms slowing water

loss in the field. Coenen-Stass (1981) found that isopods survive water loss up to 25% body mass. At the observed asymptotic rate (0.036% per hour) this would limit dispersal to 33 d. However, unsettled isopods were recaptured after longer intervals, showing that the estimated ceiling is incorrect, or that they had settled and then lost or abandoned their burrows. Higher loss rates by females are consistent with Warburg's (1987) results, and may be one source of the higher mortality observed in females in this study, who travel faster (Baker 1998), perhaps leading to the faster water loss observed here.

The intermediate peak in new burrow success as a function of time of settling suggests that costs and benefits of dispersal depend on time of emergence in the season. Isopods do not appear to be site-limited until late in the spring (Linsenmair 1984), so they should suffer less than a highly territorial species due to occupation of superior sites by the earliest settlers. However, the present results suggest that there is a penalty for settling late in the season, but no benefit to early settling above avoiding mortality during travel.

It is unlikely that the mortality experienced by traveling isopods is balanced by the probability of identifying superior habitat and establishing new burrows in those locations. The simulation prediction of  $7.1 \pm 6.4$  d (mean  $\pm 1$  SD) prior to settling, based on observed habitat variation and mortality, is similar to two seasons of observed dispersal durations, of  $6.6 \pm 6.9$  d and  $7.9 \pm 7.8$  d, in the field (Baker 1998). However, the model assumed perfect knowledge of the distribution of habitat quality from the field studies, an unlikely assumption (Baker 1998, Baker et al. 1998); thus all the variation in habitat quality was available as a benefit of movement. The model also used a low estimate of relative dispersal cost by using a high estimate from field data of mortality after settling. Both of these factors increased predicted dispersal distributions, so another potential benefit of movement is likely operating if the observed dispersal duration is adaptive. In this study isopods settled in old burrows were much more likely to succeed than those occupying new burrows. The differences observed are conservative, because all old burrows were counted as if they contained a mated pair. In fact, some old burrows were never occupied by pairs attempting to reproduce, but censuses were not carried out late enough to measure what proportion of old burrows were occupied by mated pairs following the dispersal season. In a study of habitat selection (Baker et al. 1998), isopods settled in artificial burrow holes at densities 17 times the density in unmanipulated plots. Furthermore, Linsenmair (1971) observed that males and females both readily colonized empty burrows. Study of the encounter rate and colonization success of old burrows by traveling isopods is needed to determine whether the mortality costs of not establishing a new burrow are balanced by the opportunity to colonize an old burrow. In addition, the potential costs of

digging a new burrow should be investigated to understand why old burrows are more successful.

To our knowledge, this is the first study to combine measures of incremental direct and indirect costs and benefits of dispersal in a single investigation. Observation of burrow success alone would not have revealed the high mortality costs associated with movement, and might have led to a premature conclusion that the small advantage seen by those that take longer before settling accounts for the time before settling of ranging individuals. Measurements of mortality alone do not yield much insight as to the function of movement. When they are compared to potential benefits, usually observed after settling, survival measures can be used to evaluate the explanatory power of alternative functions of movement. This study demonstrates several costs and potential benefits that depend on the amount, and not just the presence, of movement or emigration, in contrast to the simplifying assumptions of several earlier modeling approaches. Dichotomous definitions of dispersal as the opposite of philopatry perhaps obscure the continuous distributions of many species' movements. Even when philopatry is well defined, that does not imply that dispersal is a singular trait or state. Costs and benefits of dispersal must also be measured as functions of the amounts of time spent and distance moved before settling, in order to understand why animals move as far as they do.

#### ACKNOWLEDGMENTS

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#### APPENDIX A

Estimates of recapture probabilities calculated with SURGE are available in ESA's Electronic Data Archive: *Ecological Archives* E085-028-A1.

#### APPENDIX B

Estimates of survival probabilities calculated with SURGE are available in ESA's Electronic Data Archive: *Ecological Archives* E085-028-A2.