

MOVEMENT ECOLOGY: SIZE-SPECIFIC BEHAVIORAL RESPONSE OF AN INVASIVE SNAIL TO FOOD AVAILABILITY

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Abstract. Immigration, emigration, migration, and redistribution describe processes that involve movement of individuals. These movements are an essential part of contemporary ecological models, and understanding how movement is affected by biotic and abiotic factors is important for effectively modeling ecological processes that depend on movement. We asked how phenotypic heterogeneity (body size) and environmental heterogeneity (food resource level) affect the movement behavior of an aquatic snail (*Tarebia granifera*), and whether including these phenotypic and environmental effects improves advection–diffusion models of movement. We postulated various elaborations of the basic advection–diffusion model as a priori working hypotheses. To test our hypotheses we measured individual snail movements in experimental streams at high- and low-food resource treatments. Using these experimental movement data, we examined the dependency of model selection on resource level and body size using Akaike’s Information Criterion (AIC). At low resources, large individuals moved faster than small individuals, producing a platykurtic movement distribution; including size dependency in the model improved model performance. In stark contrast, at high resources, individuals moved upstream together as a wave, and body size differences largely disappeared. The model selection exercise indicated that population heterogeneity is best described by the advection component of movement for this species, because the top-ranked model included size dependency in advection, but not diffusion. Also, all probable models included resource dependency. Thus population and environmental heterogeneities both influence individual movement behaviors and the population-level distribution kernels, and their interaction may drive variation in movement behaviors in terms of both advection rates and diffusion rates. A behaviorally informed modeling framework will integrate the sentient response of individuals in terms of movement and enhance our ability to accurately model ecological processes that depend on animal movement.

Key words: advection–diffusion models; aquatic snail; body size; environmental heterogeneity; food resources; invasion; movement behavior; movement ecology; phenotypic heterogeneity; *Tarebia granifera*; Trinidad, West Indies.

INTRODUCTION

The movement of individuals is one of the fundamental components of contemporary ecological problems such as metapopulation theory, epidemic models, competitive coexistence, and other spatial models. However, despite the vital role that movement plays in these conceptual models, our understanding of the ecology of movement behaviors remains limited. Immigration, emigration, migration, and redistribution (e.g., within a population or community) provide connections between habitats, populations, and so on, via movement of individuals. Often modeled as constants in metapopulation models, or as a function of distance between sites, these movements are also affected by biotic and abiotic conditions in the vicinity of the focal animal and may be phenotype specific (Gilliam and Fraser 2001). In

the face of environmental changes (e.g., land use change, climate change, habitat loss, species extirpations, and species additions), individuals may respond to changing biotic and abiotic conditions in terms of their movement behaviors. Understanding the behavioral response to such factors often will be crucial to effectively modeling ecological processes that depend on individual movement ecology.

Previous research has shown that environmental heterogeneities affect movement (Grosholz 1996, Shigesada and Kawasaki 1997) via factors such as habitat quality (Lubina and Levin 1988, Zabel et al. 1998, Haddad 1999, Williamson and Harrison 2002, Fraser et al. 2006) and resource availability (Kareiva and Odell 1987, Arditi and Dacorogna 1988, Grunbaum 1998, Fryxell et al. 2004). We were interested in how these ecologically important factors will affect movement behaviors, and we considered how resource availability might change individual movement. For example, movement rates of individuals might hypothetically decrease through areas of higher resource level, as in an area-restricted search; however, movement rates

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might also hypothetically increase through areas with greater resource availability as individuals sense resource gradients via taxis or some other behavioral response. In addition, individuals' responses to factors such as resource availability may be phenotype specific. For example, population heterogeneity is known to influence movement behaviors via the effects of body size (Skalski and Gilliam 2000, 2003, Zabel 2002). Further, the effect of a phenotypic trait (body size) can interact with habitat characteristics (predation regime) to produce site-specific patterns of movement that differ among habitat types (Fraser et al. 2006). Thus, not only do population and environmental heterogeneities influence movement behaviors, but their interaction may also drive variation in movement behavior, requiring that we integrate these effects into ecological models that depend on movement ecology.

Here, using an advection–diffusion framework, we examine how both phenotypic variation and environmental variation affect movement behaviors in populations of exotic freshwater snails. Our interest lies both in (1) how local movement behaviors are affected by population heterogeneity (in terms of individual body size) and environmental heterogeneity (in terms of resource level) and their interaction, and (2) which components of the advection–diffusion modeling framework reflect and incorporate these behaviors. We proposed, a priori, a set of alternative movement models based on the advection–diffusion model (Okubo and Levin 2001). These alternative models represent hypotheses regarding the effects of body size and food availability on movement behaviors. We chose these factors to represent our environmental and population heterogeneities because past research suggested that body size and food availability may impact movement behaviors of gastropods (DeNicola and McIntire 1991). Using experimental movement data, we evaluate these models using information criteria (Hilborn and Mangel 1997, Burnham and Anderson 2001, 2002). Finally, we discuss the implications of these findings in regard to previous studies of movement and ecological processes that depend on movement.

MODEL

Classical advection–diffusion model

Advection–diffusion models have been used extensively to describe movement and predict population spread, including that of invasive species (Skellam 1951, Andow et al. 1990, Liebhold et al. 1992, van den Bosch et al. 1992, Shigesada and Kawasaki 1997, Okubo and Levin 2001). The classic advection–diffusion equation

$$\frac{\partial P}{\partial t} = D \left(\frac{\partial^2 P}{\partial x^2} \right) - \beta \frac{\partial P}{\partial x} \quad (1)$$

predicts the changes in density of individuals P through space x and time t , via solution of Eq. 1, where β is advection and D is diffusion. Advection describes the

change in the mean of a population, or bias in some direction (Okubo and Levin 2001), e.g., bias downstream, downwind, with or against current. Diffusion describes the variance around that mean. For this study we sought to understand how these two components, advection and diffusion, are affected by population heterogeneity and environmental heterogeneity. First we asked whether differences in movement among different body sizes, if any, were manifested via the advection component, the diffusion component, or both. Then we asked if resource level should be considered in the model or not. In this way, we discerned which components of the advection–diffusion equation, if any, are affected by, and should incorporate, population heterogeneity, with or without environmental heterogeneity, in a parsimonious model.

Population heterogeneity

We tested for the influence of population heterogeneity, in terms of snail size, measured as length, on the diffusion and advection components of movement. We incorporated snail size (length) in our models in both the advection term,

$$\beta_i = \beta_0 + (\beta_{\text{size}} \times \text{size}_i) \quad (2)$$

and the diffusion term,

$$D_i = D_0 + (D_{\text{size}} \times \text{size}_i) \quad (3)$$

where i represents an individual. For our set of models, we consider all combinations of advection and diffusion. Advection options include: (1) advection without size dependency (β), and (2) advection with size dependency (Eq. 2). Diffusion options include: (1) diffusion without size dependency (D), and (2) diffusion with size dependency (Eq. 3). Using the four possible combinations, we can determine whether one or both of the parameters depend on body size.

Environmental heterogeneity

To test for the effect of environmental heterogeneity on the variability in snail movement behaviors, we consider resource level as a treatment. In this case, we estimate diffusion and advection parameters considering resource levels or not. Thus we compare models that estimate separate diffusion and separate advection terms for different resource levels, where H = high resources and L = low resources, vs. models without resource dependency in which the same advection rate and the same diffusion rate are estimated across resource treatments.

General model structure

The most general model structure for estimating advection in our experiment, including I_1 , I_2 , and I_3 as indicator variables, is

$$\beta = [\beta_0 + \beta_0^H I_1 I_3] + [(\beta_1 + \beta_1^H I_1 I_3) \text{size} \times I_2]. \quad (4)$$

TABLE 1. Parameter combinations that make up the a priori set of candidate models for snail movement under different food resource treatments, with or without size dependency.

Model no.	No resource dependency	Low resources	High resources
1	β, D		
2	β_{size}, D		
4	β, D_{size}		
4	β_{size}, D_{size}		
5		β, D	β, D
6		β, D	β_{size}, D
7		β, D	β, D_{size}
8		β, D	β_{size}, D_{size}
9		β_{size}, D	β, D
10		β_{size}, D	β_{size}, D
11		β_{size}, D	β, D_{size}
12		β_{size}, D	β_{size}, D_{size}
13		β, D_{size}	β, D
14		β, D_{size}	β_{size}, D
15		β, D_{size}	β, D_{size}
16		β, D_{size}	β_{size}, D_{size}
17		β_{size}, D_{size}	β, D
18		β_{size}, D_{size}	β_{size}, D
19		β_{size}, D_{size}	β, D_{size}
20		β_{size}, D_{size}	β_{size}, D_{size}

Notes: The subscript “size” indicates a size-dependent effect on advection (β) or diffusion (D): β_{size} represents $\beta_0 + (\beta_1 \times size)$ and D_{size} represents $D_0 + (D_1 \times size)$. Advection reflects the change in population mean location (e.g., bias downstream, downwind, with or against current); diffusion is the variance around that mean. These models allowed examination of the effects of population and environmental heterogeneity on advection and diffusion.

Here I_1 is 1 if resources are high and 0 if not; I_2 is 1 if size (length) is included in the model and 0 if not; and I_3 is 1 if resources are included in the model and 0 if not. Similarly, the model structure for estimating diffusion, using the same notation for its indicator variables, is

$$D = [D_0 + D_0^H I_1 I_3] + [(D_1 + D_1^H I_1 I_3) size \times I_2]. \quad (5)$$

The set of candidate models consists of combinations of advection and diffusion with or without phenotypic heterogeneity (body length), and with or without environmental heterogeneity (resource level), yielding a set of 20 a priori candidate models (Table 1). Using these combinations, we identified which parameters, with resource dependency or not, depend on phenotype to describe movement behaviors for this species.

METHODS

Study system

We focused on the movement of an aquatic snail that has been introduced to habitats throughout the tropics and to portions of the subtropics. The study species, *Tarebia granifera*, was introduced to Trinidad, West Indies, at an unknown date, presumably 10–20 years ago, and we confirmed its presence in six rivers within three drainages of the Northern Range Mountains in 2001 (S. Snider and J. Gilliam, unpublished data). This parthenogenetic snail is native to Asia and India (Abbott 1952). It has been introduced accidentally

(presumably via the aquarium trade) through much of the tropics, and also purposefully to outcompete the snail intermediate host for schistosomiasis, *Biomphalaria glabrata* (Pointier 2001). As the intermediate host for a variety of trematodes, *T. granifera* is important to both ecosystem and public health, adversely impacting native species (Mitchell et al. 2000) and, in some cases, positively influencing human health (Pointier 1999, 2001, Pointier and Giboda 1999).

We collected snails from the Arima River (a fourth-order stream), which drains portions of the southern slope of the Northern Range Mountains of Trinidad, and Ramdeen Stream (a second-order stream), one of its tributaries (10°41'32" N, 61°17'36" W). At sampling sites, both streams are shallow, clear, fast-flowing, with clear pool–riffle development and varied canopy cover.

Experimental facility

Our circulating experimental stream facility consisted of six 17 m long streams constructed of six-inch (~15.2-cm) PVC rain gutters. A 125-L reservoir at the downstream end of the facility contained guppies (*Poecilia reticulata*) collected from Ramdeen Stream for mosquito control. The water was recirculated using a 0.25-horsepower (37.3-W) submersible pump and distributed through a manifold; flow rate was maintained at 1.9 cm/s to 2.3 cm/s in each of the six replicate streams. A canopy of green agricultural mesh provided partial shade, both to mimic a partial canopy and to prevent overheating of the water.

The experimental stream facility is located within 0.5 km of both the Arima River and Ramdeen Stream. We used local water pumped from the Arima River and substrates from the river to reasonably mimic the natural environment. Each stream contained a 1.5 cm layer of rinsed river sand and flat river stones, ~7 × 10 cm. We placed stones in the center of each stream every 1.0 m to inoculate streams with algae and other stream organisms and to provide natural substrate. Experimental streams flowed for two weeks prior to applying treatments.

Experimental design

We used a completely randomized design to assign two resource treatments to the six streams within the experimental facility. Experimental treatments consisted of “low” (grazed) and “high” (not grazed) treatments. We created these contrasting resource levels by allowing, or not allowing, conspecifics to graze resources prior to conducting the experiment. A barrier separated the treatment portion of the streams (the top 12 m) from the staging portion of the streams (the lower 5 m). For low-resource treatments, 20 snails (the “grazers”) were placed in the treatment portion of each stream and were allowed to graze for three days. If grazers reached the upstream end of the system, they were returned to the downstream end of the treatment zone. We moved any such grazers from the upstream end to the

downstream end just after sunrise (06:00 hours) and just before sunset (18:00 hours). High-resource treatments were simply allowed to continue building food resources in the absence of grazers. These treatments provided visually obvious differences in algal cover (green and brown layers of algae on substrate in high-resource treatment streams vs. “clean” substrates in grazed low-resource treatments), but we did not quantify the resource levels. Grazers creating the low-resource treatments were removed 24 hours prior to running the experiment.

We created individual marks using different color combinations of fingernail polish on the outer shell of each snail. Snails were 9–26 mm long, and were sorted into three size classes (small, medium, large) prior to random assignment of snails within each size class to each stream, with a total of 20 snails per stream, to assure a range of sizes in each stream. These snails were placed in the staging portion of each stream and were allowed to adjust to their environment for 24 hours. After this adjustment period, we recorded locations for each snail and removed the barrier into treatments. We then recorded the locations of each individual after three, four, and five hours; the five-hour limit reflected termination of the experiment when the first snail reached the upstream end of one experimental stream. We used only the data collected after five hours for the model selection. We used the data collected after three and four hours to assess the fit of the best model to empirical data.

Analysis of models

We estimated diffusion and advection parameters for each of the 20 models in our model set via maximum likelihood estimation using the Solver tool in Microsoft Excel (2003). We used the general likelihood:

$$L\{x|D, \beta, t, \text{size}\} = \left(\frac{P_0}{2\sqrt{\pi Dt}}\right) \exp\left[-\frac{(x - \beta t)^2}{4Dt}\right]. \quad (6)$$

Eq. 6 is the solution to the PDE shown in Eq. 1 and predicts a normal distribution with mean βt and variance $2Dt$. To compare our 20 hypotheses, we used the resulting maximum likelihood estimates to calculate Akaike's Information Criterion, AIC (Akaike 1973), specifically AIC_c for small sample size (Burnham and Anderson 2002). We also calculated Akaike weights and evidence ratios to assist in the model selection.

We also examined how a reduced set of the models fit the empirical data by plotting predicted displacements on snail body size. First, we demonstrated the fit of the best model from the candidate set to the movement data collected after three and four hours (movement data not considered in the model selection). We also chose to show an assessment of the relative model fit by comparing four of the candidate models: (1) the simplest form of the model; (2) a model that incorporates body size but ignores resources; (3) a model that ignores body

size but incorporates resources; and (4) a model that incorporates both body size and resources. This analysis allowed for comparisons of model fit, given each type of heterogeneity alone and when both heterogeneities are included in the model.

To account for the replicate nature of the experimental facility, we added a second set of models to our analysis. Replicate experimental structure is not routinely considered in AIC model selection, so we controlled for the existence of replicate experimental streams by including or not including each experimental stream as a variable in the model for each of the 20 movement models. In this way, we estimated separate advection and diffusion coefficients for each experimental stream. We compared these models with the original set of models using the same method as previously described.

RESULTS

The empirical results

Resource level dramatically affected the pattern of upstream movement, changing the qualitative and quantitative pattern of movement. At low resources (Fig. 1A–C), we observed an upstream bias and a broad distribution of the upstream population wave (mean distance moved upstream in 5 hours = 5.51 m, SE = 0.61, SD = 4.67, pooled across replicates; Table 2). The movement distributions showed no skewness (skew = -0.05, SE = 0.31, $n = 59$, $P = 0.87$) and did show platykurtosis (kurtosis = -1.70, SE = 0.61, $n = 59$, $P < 0.01$; Table 2). In stark contrast, individuals moved in concert as a narrow wave at high resources (Fig. 1D–F), while still showing the upstream bias also observed at low resources (mean distance moved in 5 hours = 7.26 m, SE = 0.25, SD = 1.91 m, pooled across replicates; Table 2). This distribution was negatively skewed (skew = -2.28, SE = 0.31, $n = 60$, $P < 0.01$) and leptokurtic (kurtosis = 6.49, SE = 0.61, $n = 60$, $P < 0.01$; Table 2). This contrast in pattern was evident across replicates (Fig. 1, Table 2).

By examining the relationship between distance moved and snail length, we saw that the different movement behaviors observed at high and low resources were created by differences in the strength of size dependency in movement (Fig. 2). At low resources, there was a positive relationship between body size and distance moved, with large individuals moving faster than small individuals (Fig. 2A–C). A decidedly different pattern emerged for the relationship between body size and distance moved at high resources: the narrow wave of movement exhibited in the population-level distributions (just described) arose because individuals moved in concert despite differences in body size (Fig. 2D–F). It appeared that, at high resources, larger individuals slowed and smaller individuals sped up, relative to movement at low resources. Examination of the data on size-specific movement also aids in understanding the platykurtosis observed in the low-resource treatment:

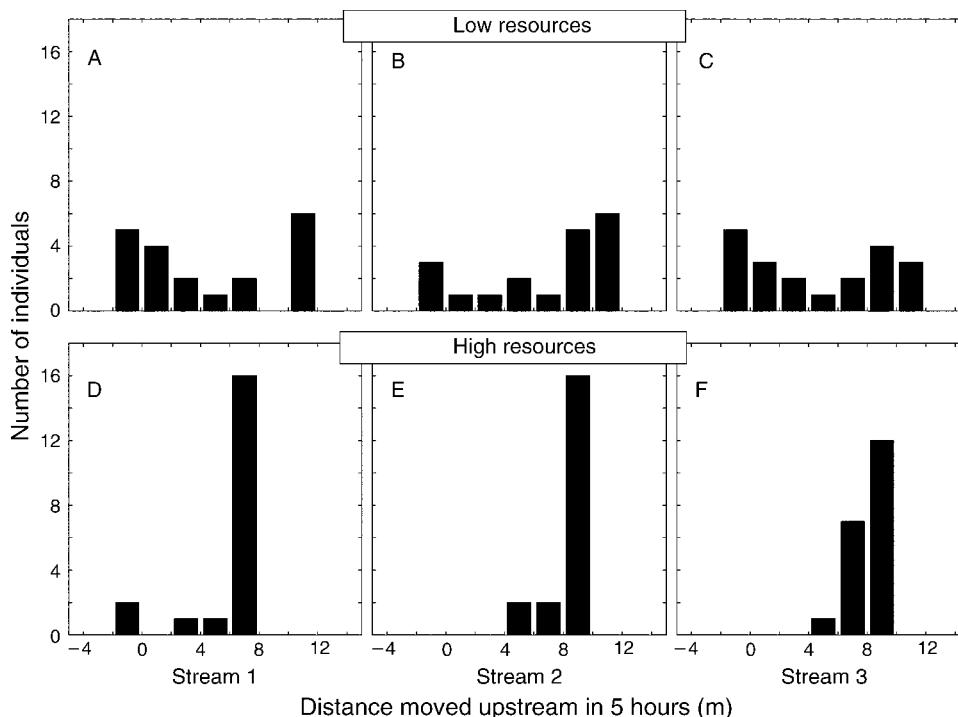


FIG. 1. Movement distributions produced by snails ($n = 20$ snails stocked per stream) in the experimental facility over five hours under low- and high-resource (food) treatments. The data are presented per experimental stream (three streams per treatment) to illustrate the consistency of results across stream units within each treatment. (A–C) Distance moved at low resources, showing an upstream bias and population spread around the mean. (D–F) Distance moved at high resources, showing a distinctly narrower upstream wave.

summations of multiple approximately normal distributions of approximately equal sample size (one distribution for each snail size or size class) can result in a platykurtic distribution overall. Thus, heterogeneity in advection rates for different size classes can yield platykurtosis. In contrast, heterogeneity in diffusion rates produces leptokurtic distributions (Skalski and Gilliam 2000, Rodriguez 2002). The skew at high resources results from a few of the smallest snails failing to maintain the upstream pace of the rest of the snails.

Alternative movement models

Of our candidate models, the top-ranked model (model 10) incorporated size dependency in advection rates, but not diffusion rates, across both resource levels (Table 3). Therefore, these data reflect population heterogeneity in advection, but not diffusion. This model also specified that advection rates and diffusion rates be estimated separately for different resource levels. Thus, the model includes a size-dependent advection rate

TABLE 2. Estimates of skewness and kurtosis, mean, and variance of the movement distributions produced by snails in each experimental stream and pooled across replicate experimental streams, under low- and high-resource treatments.

Resource level and stream	Skewness			Kurtosis			Distance moved upstream (m)	
	Skew	SE	n	Kurtosis	SE	n	Mean \pm SD	Variance
Low								
1	0.33	0.51	20	-1.92	0.99	20	9.95 \pm 9.99	29.89
2	-0.99	0.52	19	-1.06	1.01	19	9.02 \pm 9.28	18.39
3	0.19	0.51	20	-1.93	0.99	20	9.63 \pm 9.58	20.95
Pooled	-0.05	0.31	59	-1.90	0.61	59	5.51 \pm 9.69	21.83
High								
1	-2.29	0.51	20	9.15	0.99	20	5.9 \pm 2.21	9.89
2	-2.39	0.51	20	9.99	0.99	20	8.11 \pm 1.16	1.35
3	-2.11	0.51	20	5.19	0.99	20	9.96 \pm 1.29	1.13
Pooled	-2.28	0.31	60	6.49	0.61	60	9.26 \pm 1.91	3.64

Notes: Sample size (n) represents the number of individuals. In one case, $n = 19$ due to loss of one individual during the experiment.

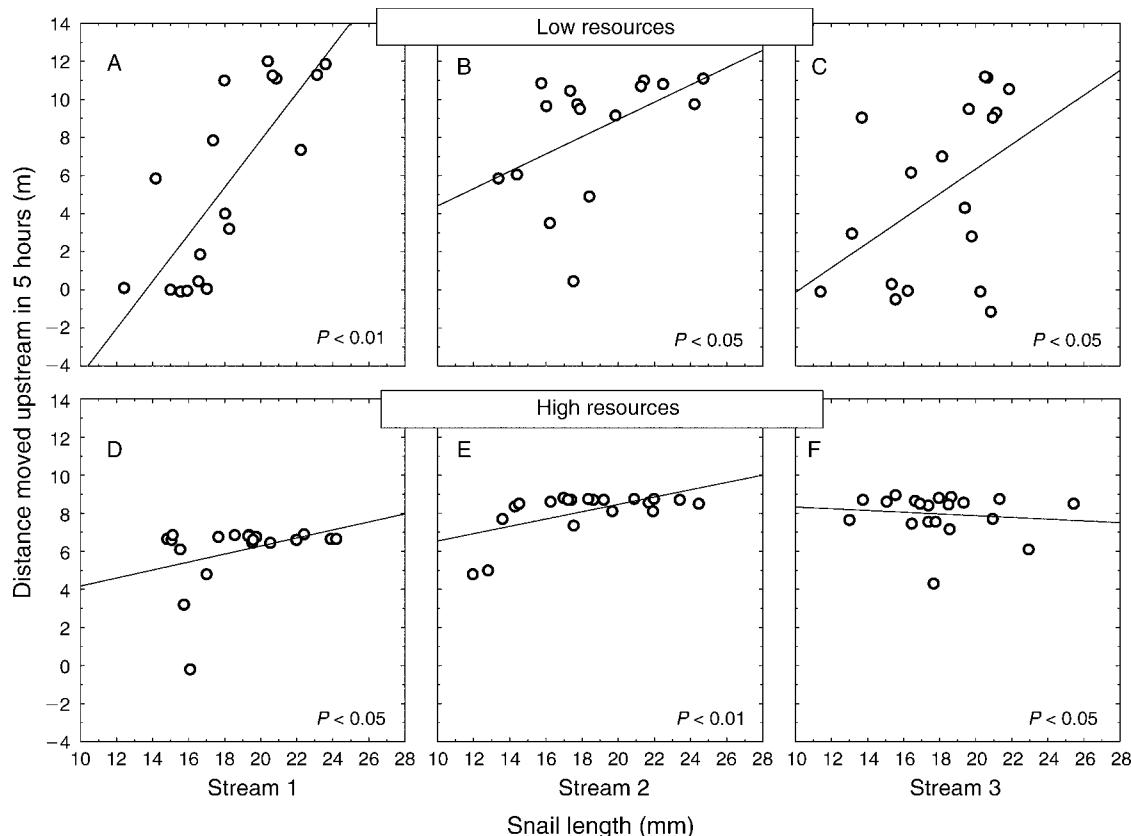


FIG. 2. The relationship between distance moved and body size (length) in each of the experimental units. (A–C) At low resources, there is a positive relationship between distance moved and body size (slopes of linear regression lines are significantly different from zero at the levels shown in each panel). (D–F) At high resources, most individuals moved upstream at a similar rate despite differences in body size, resulting in the narrower wave seen in Fig. 1 (slopes of linear regression lines are significantly different from zero in panels D and E; *P* values given).

TABLE 3. Top-ranking candidate models for the effects of body size and resource level on snail movement in an advection–diffusion framework.

Model no.	Model description		log(<i>L</i>)	<i>K</i>	AIC _c	Δ _{<i>i</i>} AIC _c	<i>w_i</i>	Evidence ratio	Model rank
	Low resources	High resources							
10	β_{size}, <i>D</i>	β_{size}, <i>D</i>	–285.46	6	583.67	0.00	0.489	1.00	1
18	β_{size}, <i>D</i>_{size}	β_{size}, <i>D</i>	–285.25	7	585.52	1.85	0.194	2.52	2
9	β_{size}, <i>D</i>	β, <i>D</i>	–287.52	5	585.57	1.91	0.189	2.59	3
17	β _{size} , <i>D</i> _{size}	β, <i>D</i>	–287.32	6	587.38	3.71	0.076	6.40	4
12	β _{size} , <i>D</i>	β _{size} , <i>D</i> _{size}	–287.26	7	589.53	5.86	0.026	18.76	5
Experimental unit as variable:									
10	β_{size}, <i>D</i>	β_{size}, <i>D</i>	–259.76	18	562.36	0.00	0.937	1.00	1
9	β _{size} , <i>D</i>	β, <i>D</i>	–266.85	15	568.35	5.99	0.047	20.03	2

Notes: The subscript “size” indicates a size-dependent effect on advection (β) or diffusion (*D*); see Table 1. Clearly, a size-dependent advection rate is consistent across the top-ranked models in this set. Explanation of column headings: log(*L*) is the log likelihood estimate, *K* is the number of parameters, and AIC_c is the corrected Akaike’s Information Criterion; Δ_{*i*}AIC_c is the difference between the lowest AIC_c score and the AIC_c score of each model (model *i*); Akaike’s weight (*w_i*) is the weight of evidence in favor of model *i*; the evidence ratio is the number of times more likely the top-selected model is relative to model *i* (e.g., model 1 is 2.52 times more likely than model 2). Boldface indicates models that were accepted as plausible (ΔAIC_c < 3). The second section of the table shows results of the second model selection in which we controlled for the replicate nature of the stream facility by including the experimental unit as a variable in the models.

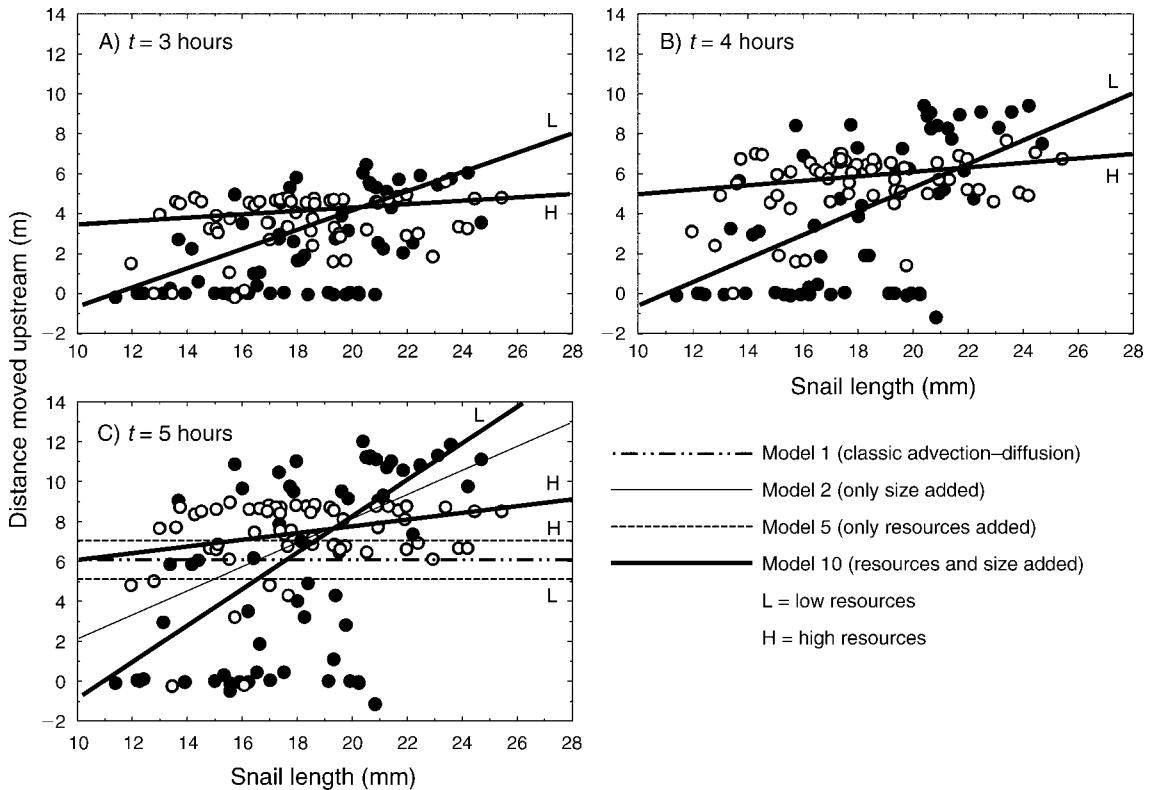


FIG. 3. Model predictions overlaid on the relationship between the distance moved and body size after (A) 3, (B) 4, and (C) 5 hours, pooled across replicate streams. Solid circles indicate low-resource treatments, and open circles represent high-resource treatments. Lines represent model predictions for four models from the a priori set of models. Models that are resource dependent (models 5 and 10) produce two prediction lines: one for low resources (L) and one for high resources (H). Model 1 is the simplest model, predicting that all snails move upstream the same distance despite differences in body size or resource level. Model 2 represents predictions from a model that incorporates body size in advection, illustrating a positive relationship between distance moved and body size, but no discrimination for resource level. Model 5 predictions illustrate the effect of including resources, but not size, in the model: snails respond to resource level, but at a particular resource level they move the same distance despite differences in body size. Finally, model 10, the AIC best model from our a priori set of models, shows predictions given size-dependent advection plus resource dependency, and captures an interaction between the effect of resource level and the effect of body size at each time.

for movement at low resources (two parameters), a size-dependent advection rate for movement at high resources (two parameters), a diffusion rate (size-independent, one parameter) for movement at low resources, and a diffusion rate (size-independent, one parameter) for movement at high resources (six parameters total).

Although model 10 is the top-ranked model in our analysis, according to evidence ratios, this model had only 2.52 times more support than the next most likely model (model 18) and only 2.59 times more support than model 9 (Table 3). Going beyond the top-three-ranked models, we see a distinct jump in the support for the first three models (models 10, 18, and 9) relative to the remaining ranked models, which received much less support in terms of evidence ratios. Due to model selection uncertainty, we accepted the top-three-ranked models ($\Delta AIC_c < 3$) as plausible (Burnham and Anderson 2002). Size dependency and resource dependency are supported across the plausible models. Models

that did not incorporate size dependency into some aspect of advection received no support. More specifically, models that did not incorporate a size-dependent advection rate at low resources received no support. We also rejected all models that were not resource dependent. Size dependency in diffusion received only weak support (model 18, for low resources). Overall, the three top models collectively support the top-ranked model: size-dependent advection that depends on resources, and size-independent diffusion that depends on resources.

In Fig. 3, we examine how model 10 captures features of the data that simpler models do not, and also how model 10 fits data from previous time periods. At the completion of the experiment ($t = 5$ hours), it is clear that, although none of the models appears to totally characterize the variation in movement, model 10 is certainly the best of this set because it provides for patterns of movement resulting from an interaction of body size and response to resource level: one pattern at

high resources where individuals move upstream together regardless of body size, and one at low resources where there is a positive relationship between predicted distance moved and body size. The other models presented here cannot capture that interaction between phenotype and environment, because they include at most one of those factors. In our view, model 10, which was fit only with data for $t = 5$, also reasonably modeled the data for $t = 3$ and $t = 4$, because the patterns seen for $t = 5$ are developed. However, these plots also reveal a phenomenon that none of the candidate models could capture: the apparent trend toward a bimodal distribution in the low-resource environment, generating the positive kurtosis values observed in the movement distributions. Model 10 did capture the fact that the largest snails tended to move upstream (all snails >21 mm moved strongly upstream), and that the smallest snails did not, via the modeling of advection as a linear function of body size. However, none of the a priori candidate models had the flexibility to incorporate the apparent development of a bimodal distribution that developed at low resources, with some individuals not moving upstream and others doing strongly so, in contrast to the high-resource treatment, in which almost all individuals moved upstream in concert. The mechanism(s) leading to development of that bimodality at low resources but not high resources is worthy of further investigation, but here we restrict ourselves to assessment of the a priori model set.

When we included “stream effects,” i.e., the effects of using replicate experimental streams to collect data, in our model, AIC scores were lower than when we did not incorporate these effects, despite a much higher number of parameters under penalty in AIC. Hence, including replicate structure in AIC model selection provided some amount of improved fit of the models to the data. The movement patterns observed across replicates in Figs. 1 and 2 appear very similar for each resource treatment, suggesting that this model selection process was sensitive even to very slight differences in movement patterns (i.e., deviations of one or two individuals from the prevailing pattern) across replicates. Remarkably, including stream effects in the models had little effect on the ultimate model choice in terms of our parameters of interest (Table 3). Of the candidate models in this case, the top-ranking model is still the one that includes size dependency in advection rates and resource dependency in both advection and diffusion. Model 10 also had 20 times more support than model 9 in this case, and we therefore accept only model 10 as plausible in this analysis.

DISCUSSION

Patterns from empirical data

By changing the way that phenotype (body size) responded to the environmental variable (food resources), different resource levels created strikingly different movement patterns for *Tarebia granifera*. At low

resources, we observed a clear correlation between size and mean distance moved (Fig. 2A–C), contributing to a broad and distinctly platykurtic distribution of movement by the population as a whole (Fig. 1A–C, Table 2). At high resources, in contrast, the effect of body size disappeared and individuals moved upstream together at a similar rate, as a narrow wave (Fig. 2D–F). The environment–phenotype interaction that we found involving resources and body size has also been shown to be important to the movement behavior of a tropical killifish, *Rivulus hartii*, under different predation regimes (Gilliam and Fraser 2001, Fraser et al. 2006) and in migrating salmon (Zabel 2002). In the predator–prey study, researchers showed that body size can interact with level of predation threat, changing movement behaviors in different habitat types (Gilliam and Fraser 2001, Fraser et al. 2006). Similarly, Zabel (2002) modeled travel time, or migration duration, of chinook salmon (*Oncorhynchus tshawytscha*). Results of his study indicated that both body size and current velocity, and their interaction, were contributors to the variability of animal movement patterns (Zabel 2002). Predation threat, current velocity, and other biotic and abiotic factors not addressed in this study might also affect movement behavior in natural settings.

The narrow wave of movement at high resources occurred because smaller individuals moved faster, and larger individuals moved more slowly, than individuals of equivalent size at low resources. We have not yet studied the microscale, behavioral mechanisms producing this pattern. One possibility is an area-restricted search, in which larger individuals slow down given high food resources, and small individuals speed up through areas where food resources have been reduced, *sensu* Kareiva and Odell (1987). Previous studies have shown that this foraging behavior can result in resource-mediated grouping behaviors predicted theoretically (Wilson and Richards 2000) or “density-dependent migratory waves” illustrated with large-scale empirical data (Fauchald et al. 2006). Given the strong directional bias in this species, we are reluctant to assume an area-restricted search hypothesis with turning rate as its mechanism, but some behavioral response to resource gradients, with steeper or more detectable gradients in the high-resource case, would appear to be involved. Although our model depicts movement by snails as independent of other snails, a different model incorporating interaction via resources or responses to chemical cues generated by the activities of conspecifics is worthy of attention. Also, although we used body size as the phenotypic trait in these models, traits such as competitive characteristics, or other traits correlated with body size, might underlie the differences that we model as being attributable to body size; traits such as hunger level, reproductive state, and others might, of course, be used to further improve model performance.

Because our low-resource treatments were previously grazed, but our high-resource treatments were not, our

empirical results may have implications for understanding movement behavior at the front of an invading population. We can label the high-resource treatment as an “uninvaded” habitat and the low-resource treatment as a “previously invaded” habitat. Viewed in this context, this species exhibited a behavioral response at the front of the invasion in the “uninvaded” habitat, resulting in a narrow population wave for a broad array of sizes at the invasion front when compared to movement in the “previously invaded” habitat. Given previous work showing sensitivity of invasion speed to demography at the edge of the invasion (Neubert and Caswell 2000), attention to behavioral influences on population composition at the edge of a spreading population should improve predictive models of invasive spread. Also, based purely on population dynamics, without heterogeneity in phenotype or flexible behavior, Sherratt et al. (Sherratt et al. 1997, Sherratt 2001) has shown production of periodic traveling waves as an invading predator interacts with a prey population. The changes in the width of the wave that we observed occurred purely due to behavioral response to different levels of resources (prey) without involving population dynamics, whereas Sherratt et al. (1997) and Sherratt (2001) found waves purely due to population dynamics without considering flexible behavior. Linking these two phenomena, and asking when and how the two processes interact, could also improve our predictive capacity in spatially interacting predator–prey systems.

*Phenotype- and environment-specific behavior
is needed in movement models*

Our findings showed that population heterogeneity not only impacts movement behaviors (Price et al. 1994, Oriain et al. 1996, Paradis et al. 1998, Skalski and Gilliam 2000, 2003, Fraser et al. 2001, Gilliam and Fraser 2001, Langellotto and Denno 2001, Rodriguez 2002, Zabel 2002, Coombs and Rodriguez 2007), but also may impact components of movement models in different ways. The model selection exercise indicated that the effect of population heterogeneity is best described via the advection component of movement: the top-ranked model was one that included size dependency in the advection rate, but not in the diffusion rate. For any given species, predictions about the impact of population heterogeneity on movement patterns will depend on which component(s) of movement are most affected by phenotypic variation. Further, the role that population heterogeneity plays in structuring population-level patterns of movement in an advection–diffusion framework may interact with environmental heterogeneity, as we found here. Given that a separate advection coefficient should be used for these data at high and low resources, and given the size dependency in the advection rates, the magnitude of the influence of population heterogeneity was context dependent. Thus population and environmental heterogeneities both influence movement behaviors and their

interaction may drive variation in movement behavior in terms of both advection rates and diffusion rates.

Finally, we emphasize the importance of the advection component for modeling movement of these exotic snails when using an advection–diffusion framework. In this species, we observed a strong upstream bias in the movement distributions that is reflected in the model selection results. This upstream bias by this species also occurs in natural streams, as revealed by mark–recapture studies (S. Snider, *unpublished data*). Although neither advection nor diffusion terms could be considered constant across all sizes and environments, the size-dependent advection rate was consistent across the top-ranked models in our set, suggesting that the observed movement patterns are consistently influenced by the advection component in this framework. Further research addressing the consequences of different advection rates relative to diffusion, and the impact of other biotic and abiotic factors on advection, would be helpful for accurately modeling the movement ecology of this species.

On the utility of advection–diffusion models

The simple diffusion model is often criticized for its simplicity, yet it has been used extensively to model and, perhaps, to understand movement in the context of invasive spread (Holmes 1993, Shigesada and Kawasaki 1997, Okubo and Levin 2001). Following earlier work by Fisher (1937) and Skellam (1951), it has been utilized to describe the spread of many different organisms in various environments (Lubina and Levin 1988, Andow et al. 1990, Liebhold et al. 1992, Holmes 1993, Skalski and Gilliam 2000, Okubo and Levin 2001, Zabel 2002, Fryxell et al. 2004). Although there is a substantial scientific literature that expands on the simple diffusion model (van den Bosch et al. 1990, 1992, Holmes 1993, Kot et al. 1996, Neubert and Caswell 2000) and related approaches using random walks (Morales et al. 2004, Jonsen et al. 2006), we chose to focus on understanding how population and environmental heterogeneities are incorporated into the two components of this simple, yet arguably elegant, form of the model.

The simple advection–diffusion equation is criticized because, in part, its assumptions are not achievable by any organism (Turchin 1998). First, the model arose from a mathematical derivation that assumes that dispersal occurs randomly at an infinite velocity throughout every stage of an organism’s life. This assumption is never met; not only is movement not infinitely rapid, but also many organisms have life stages or phenotypes that differ in dispersal rate, and animal dispersal follows from behavioral decisions rather than non-sentient wandering (van den Bosch et al. 1992, Holmes 1993, Shigesada and Kawasaki 1997). Although these common criticisms are cited against the simple diffusion model, and we ourselves have shown that the simplest model performs poorly, we do not advocate eliminating this basic modeling framework from the set

of tools we use to understand and model movement behaviors and population spread. In many cases, and for particular purposes, even the simplest advection–diffusion model has been shown to provide satisfactory estimations of population redistribution for many species (Skellam 1951, Kareiva 1983, Lubina and Levin 1988, Andow et al. 1990, Okubo and Levin 2001), and the assumptions of the model are not as severe as they appear. Holmes (1993) points out that the assumptions are valid only on “infinitesimal scales,” and that on a more practical level the consequences of the assumptions are slight. Comparing telegraph models with the simplest advection–diffusion model, Holmes (1993) concluded that for particular parameter values and for some classical examples of invasive spread, the simple advection–diffusion model performed as well as the more complicated alternative. Also, the random walk assumption does not necessarily require that individuals move randomly; rather, it requires that at the population level, movement distributions mimic the distribution produced by randomly moving individuals, and this relaxation of the assumption can sometimes allow for navigation or intelligent moves by individuals (Lubina and Levin 1988). Finally, the homogeneous form of the advection–diffusion equation predicts a Gaussian distribution, but modeling the total population as mixtures of normal distributions can produce leptokurtic or other distributions often observed in nature (Skalski and Gilliam 2000, Okubo and Levin 2001, Morales 2002). Therefore the basic model is flexible enough to consider population heterogeneities via extensions.

One final criticism of the simple advection–diffusion model is that it does not predict long-distance moves. Modeling has indicated that rare long-distance dispersal events ultimately determine invasion speed (Kot et al. 1996, Clark 1998, Neubert and Caswell 2000). However, diffusion models with population heterogeneity in behavior easily produce arbitrarily strongly leptokurtic dispersal kernels (e.g., Skalski and Gilliam 2000), allowing use of the diffusion approach or any of several alternatives in many cases (Coombs and Rodriguez 2007), while explicitly modeling individual differences in behavior rather than treating dispersal kernels as a purely phenomenological component of the model. In the present study, we chose to focus on movement over a short spatial scale, and how advection and diffusion reflect animal behavior within that scale. However, expanding such studies to larger spatial and temporal scales to explore and compare the usefulness of advection–diffusion or other approaches in behaviorally informed models remains a useful area of research.

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