

Seasonal source–sink dynamics at the edge of a species' range

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Abstract. The roles of dispersal and population dynamics in determining species' range boundaries recently have received theoretical attention but little empirical work. Here we provide data on survival, reproduction, and movement for a Virginia opossum (*Didelphis virginiana*) population at a local distributional edge in central Massachusetts (USA). Most juvenile females that apparently exploited anthropogenic resources survived their first winter, whereas those using adjacent natural resources died of starvation. In spring, adult females recolonized natural areas. A life-table model suggests that a population exploiting anthropogenic resources may grow, acting as source to a geographically interlaced sink of opossums using only natural resources, and also providing emigrants for further range expansion to new human-dominated landscapes. In a geographical model, this source–sink dynamic is consistent with the local distribution identified through road-kill surveys. The Virginia opossum's exploitation of human resources likely ameliorates energetically restrictive winters and may explain both their local distribution and their northward expansion in unsuitable natural climatic regimes. Landscape heterogeneity, such as created by urbanization, may result in source–sink dynamics at highly localized scales. Differential fitness and individual dispersal movements within local populations are key to generating regional distributions, and thus species ranges, that exceed expectations.

Key words: *Didelphis virginiana*; distribution edge; individual fitness; landscape heterogeneity; life table; metapopulation; range limit; source–sink dynamics; urbanization; Virginia opossum.

INTRODUCTION

What determines species' distributional boundaries? One of the oldest questions in ecology, this remains one of the most enigmatic, despite immediate relevance to conservation given current habitat fragmentation and climate change. We expect species' range limits to be shaped by proximate mechanisms acting on populations at the distributional edge (Thuiller 2004, Parmesan et al. 2005), but we know little about these populations. Despite considerable theoretical attention, field data on births, deaths, and movements of individuals at a species' range margin are sparse (Holt et al. 2005, Sagarin et al. 2006). Here, we present the demographics of Virginia opossums (*Didelphis virginiana*) at a local distributional edge, and suggest that observed source–sink dynamics explain both local range limitation and regional range expansion.

By definition, at a range edge, a species is encountering the boundary of its realized niche, and this phenomenon can be viewed from multiple spatial scales. At large

scales, the long-standing “abundant center model” hypothesizes that a species will be most abundant at the center of the range where environmental conditions for the species are most ideal (Andrewartha and Birch 1954, Brown 1984, Samis and Eckert 2007). As environmental conditions change along geographic gradients, so does suitability for the species and the species becomes less common (Brown 1984). In an offshoot of this theory, range edges have been predicted to act as peripheral sinks that absorb individuals from more central source habitat (Guo et al. 2005, Holt et al. 2005).

Treating the range as a metapopulation, we may imagine at the range edge populations occupying discrete patches that become less and less frequent in an unoccupied surrounding matrix. Theoretically, range boundaries can form through metapopulation dynamics of colonization and extinction (Holt et al. 2005). Extinction probability linked to a gradual underlying environmental gradient may result in relatively abrupt range edges (Lennon et al. 1997), or edges may even be formed with edge populations in high-quality patches, if these patches are isolated (Bahn et al. 2006).

Not all occupied patches have to be able to support a stable population (Pulliam 1988). Interspersion of source populations in a fragmented landscape may sustain species presence in otherwise unsuitable neigh-

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boring habitat (Pulliam and Danielson 1991) so regional distribution patterns may not reflect the extent of habitat capable of maintaining the species. Emigration and immigration rates among habitat patches also can be misleading; it is unclear whether immigrants are selecting higher-quality habitat, or are “excess” forced into marginal habitat. At a local, within-landscape, scale, source and sink may vary by individual territories (Breininger and Carter 2003), and empirical examination of individual fitness is required to differentiate them. Unfortunately, the complex demographic data needed to address source-sink dynamics is difficult to obtain, and relatively few empirical studies have been done on source-sink dynamics (see Pulliam 1996, Breininger and Carter 2003, Lowe et al. 2006), let alone linking these dynamics to a species’ range (Thomson 2007).

We used a within-landscape approach to elucidate the interacting factors that determine the northern distributional limit of the Virginia opossum. The only marsupials established in North America, Virginia opossums have expanded their range northward in historical times, and now persist in northern areas where they would be expected to be limited by winter-induced mortality (Brocke 1970, Kanda 2005a). The Virginia opossum is a poor thermoregulator, and depends on body stores to survive freezing weather (Brocke 1970, Pippitt 1976, Hsu et al. 1988). Based on the winter energetics of opossums in Michigan, Brocke (1970) suggested that opossums had reached the northern limit set by winter temperatures. However, the species has continued to expand its range northward, particularly in New England (Gardner and Sunquist 2003). Winter survival of subadult females (the primary breeding cohort) is theoretically too low to maintain populations in central Massachusetts (or further north) because the females are too small (<2.5 kg) for their energy reserves to outlast the winter (Kanda 2005a).

Because the opossum’s distribution in central Massachusetts is locally associated with human-dominated landscapes (Kanda et al. 2006), we suggested that opossums are obligate human commensals in northeastern North America, using anthropogenic resources to expand their range into otherwise unsuitable environmental conditions. We predicted opossums that use anthropogenic resources have higher fitness than those that do not because these resources are required for over-winter survival. We also expected that surviving individuals form a source population that annually replenishes local sinks in neighboring “natural” landscapes. We monitored the survival, reproduction, and cause-specific mortality of female opossums in central Massachusetts to directly assess population dynamics at the local distributional edge, and used population and geographic models to interpret these dynamics on the landscape.

METHODS

Study site

Fieldwork was conducted in the Connecticut River Valley of central Massachusetts, USA, a mosaic of

residential and agricultural land containing fragments of mixed coniferous-deciduous forest. No opossums were captured in the more forested Pelham Hills to the east, effectively confining the study to the valley floor (for greater detail, see Kanda 2005b).

Capture and monitoring

We captured opossums either in wire-cage traps or by hand, and recorded their sex, age, and mass, along with the number, age, and sex of young in the pouch (procedures reviewed by Gardner and Sunquist 2003). We marked all animals >60 days old with passive integrated transponder (PIT) tags (Biomark, Boise, Idaho, USA), and put radio collars (35 g, Advanced Telemetry Solutions, Isanti, Minnesota, USA) on all females >0.9 kg. We also collared subadult (<1-yr-old) males when we had sufficient equipment. As possible, we located radio-tagged animals every 24–72 hours and recaptured them once a month, except during winter. After an animal died, we retrieved the body for necropsy.

We categorized habitat as being anthropogenic or natural. Anthropogenic habitats included human structures used for denning sites, foraging areas adjacent to buildings, and food resources such as garbage cans, bird feeders, outdoor pet food, and corn crops. We used the term “urban” for an opossum that included such anthropogenic resources within its home range.

Parameter analysis

We pooled reproductive data from all animals regardless of habitat to estimate overall litter size and sex ratios. Sex ratios were compared to parity with chi-square tests. For young raised in identified habitats, we compared birth dates by habitat with a two-tailed *t* test (equal variance).

We estimated survival of juveniles in the pouch (0–70 days) based on the minimum number alive. We obtained survival rates for juveniles during weaning (70–98 days) and first independence (98–126 days) with the Cormack-Jolly-Seber technique applied to mark-recapture data (Program MARK; White and Burnham 1999). We pooled males and females in these analyses, assuming mortality was not dependent on sex.

Mortality risks for radio-collared females from each habitat were compared using Cox proportional hazards regression (SAS v.8, SAS Institute, Cary, North Carolina, USA) in each of three seasons (breeding, 15 April–30 August; autumn, 1 September–30 November; winter, 1 December–14 April), and grouped by age (subadults, 1-yr-olds, and 2-yr-olds). We included males in the subadult autumn analysis after quantifying the effect of sex on survival. We used *t* tests to examine habitat-specific differences in subadult female mass and age at the onset of winter.

We generated maximum likelihood estimates (MLE) of survival and cause-specific mortality rates for each age group by season (micromort; Heisey and Fuller

1985). Four types of rates were calculated: (1) cause-specific mortality, (2) survival, (3) persistence, and (4) persistence adjusted for sample-size bias. The survival rate for a population within a habitat was estimated with dispersal out of that habitat treated as a censor. This rate reflects the probability of not dying within a habitat for the period. Persistence rate, in contrast, reflects the probability of an animal neither dying nor moving out of the habitat; in this calculation dispersal is one of the competing risks. Theoretically, persistence plus dispersal equals within-habitat survival; however, there was not an exact correspondence. Finally, we also calculated persistence rates correcting for sample-size bias. The MLE for interval rates inflates when sample size is small, but the statistical bias can be approximated and the point estimate adjusted accordingly (Heisey and Fuller 1985). Uncertainty estimates throughout are SE unless otherwise indicated.

Life-table model

Point estimates of reproduction, persistence, and dispersal in each habitat were incorporated in a model with discrete time steps in an annual cycle. Since spring dispersal from urban habitat occurred early, we structured the model with dispersal first and then used the survival rather than persistence rate for non-dispersing urban individuals. In autumn, dispersal occurred throughout the season, so we assumed that dispersing individuals were, on average, in the adopted habitat for half of autumn (dispersing animals de facto survived until dispersal, then risked death but not dispersal in their new habitat for half the period). Although dispersing individuals moved between two habitats within the model, the total model population was closed. The model was iterated to stabilize the structure and obtain a total annual per capita population growth rate (λ).

A second model was parameterized with the bias-adjusted persistence rate point estimates. Large confidence intervals are a classic problem in survival rate estimation (Heisey and Fuller 1985), so we built a third model informed with parameter estimates from the literature (reviewed by Gardner and Sunquist 2003, Kanda and Fuller 2004). We used the point estimates from the original model, but truncated the 95% confidence intervals if they exceeded minimum or maximum literature estimates.

We recognized that we could not parse spatiotemporal and sampling variation for this study, so we used the uncertainty estimates to explore the potential variation in population growth rate under the study conditions. For each of our three models (original, bias-adjusted, and literature-informed), we varied the parameters using Monte Carlo simulation (coded in Visual Basic; Microsoft, Redmond, Washington, USA; Supplement). In each simulation run, each parameter was drawn randomly from its uncertainty distribution (normal except for MLE persistence rates which were log-

normal; see Heisey and Fuller 1985). From 10 000 simulation runs for each of the models we calculated the average λ and its 95% confidence interval after normalizing the distribution with a fourth-root transformation. For the original parameter model, we recorded the simulated parameters and λ . In SAS, we used a full-model regression analysis of the parameters on λ to obtain partial r^2 values as measures of the population growth rate response to the uncertainty in the parameters.

We examined the sensitivity of λ to the parameters in the original life-table using two methods. First, we used a "static" method where we allowed only the parameter of interest to vary, recording the parameter and λ for 1000 simulations. Second, in the "stochastic" method, we allowed all parameters to vary each run except the one of interest. This parameter was fixed, and 10 000 runs generated an average λ for that parameter value. We then altered the parameter to a new fixed value, conducted 10 000 runs, and calculated a new average λ . In both methods, sensitivity was calculated as the change in λ for a change of 0.1 (or 10%) in the parameter.

Geographic prediction

We defined urban and natural habitat in the Connecticut River Valley of central Massachusetts based on land-use classification from the Southern New England Gap Analysis Project (SNEGAP; Slaymaker et al. 1996). We considered suburban or urban SNEGAP GIS layers (codes 168, 184, 212, and 213) as development. In Arcview GIS (ESRI, Redlands, California, USA), we classified development plus a 100-m buffer as urban habitat. The buffer accounted for typical movements of animals that used anthropogenic resources but also included natural areas within their ranges. We divided the simplified habitat map into 1-km² units using the UTM grid.

The life-table model provided a ratio of breeding females in each habitat when the model structure was stabilized through iteration. We modified that ratio to account for population growth, assuming that urban habitat was saturated and population expansion would therefore increase the number of natural habitat females. The adjusted ratio of breeding females reflected the predicted ratio of breeding females in each habitat for a total stable ($\lambda = 1$) population. We estimated the habitat-specific home-range size of breeding females using radiotelemetry locations in Arcview GIS 3.3 and the 95% kernel estimation technique (Hooge et al. 1999). From these, we calculated the density of females (animals/km²) in each habitat type while breeding. We then used these densities to translate the ratio of females for each habitat into r , the predicted ratio of occupied natural habitat to occupied urban habitat in a stable population.

To determine the population status for each km² unit, we compared the ratio of natural and urban habitat in

TABLE 1. Theoretical population units for the geographical model.

Unit type	Initial condition	Condition with immigration	Description
Source	$K_0 > 1$		Sufficient urban habitat present in unit for unit population to grow, producing emigrants.
Stepping-stone sink	$K_0 < 1$	$K_1 > 1$	In isolation, unit population would decline; with annual immigration from nearby source areas, population will grow and produce emigrants.
Sink	$K_0 < 1$	$s \geq 2$ urban home range or $K_1 - K_0 \geq 2$ natural range or $s \geq 1$ urban range and $K_1 - K_0 \geq 1$ natural range	Occupied consistently by at least two breeding females, but will not produce emigrants and in isolation would decline.
Itinerant	$K_0 < 1$		Within 10 km of a source or sink, such that an occasional disperser could arrive, but would not be expected to replace itself.
Unoccupied	$K_0 < 1$		>10 km from any breeding populations, no individuals are expected.

Notes: K_0 is the value assigned to a 1-km² unit reflecting the area of natural habitat that could be occupied by opossums produced from the unit. K_1 is K_0 adjusted for the effect of immigration into the unit. The value s reflects the area of urban habitat within the unit.

the unit with the occupation ratio from the life-table model. We assigned a growth value K to each 1 km² as $K = r \times s - (1 - s)$ where s was percentage of urban habitat in a unit and $(1 - s)$ was percentage of natural habitat. K could range from -1 to r , and represented emigrants generated by the unit (or immigrants that could be absorbed into the unit), as measured in square kilometers of natural habitat. K equaled 0 when the ratio of natural to urban habitat ($(1 - s)/s$) in a 1-km² unit was equal to the ratio of natural to urban habitat predicted for a stable population by the life-table model (r). This meant the unit would be saturated with opossums in both urban and natural habitat, and the resident opossums would form a stable population. Positive K values represented sources (Table 1), and were apportioned to adjacent non-source units (Fig. 1). Contiguous source units were treated as a single area. Units starting with a negative K would experience population decline if they were isolated populations. These were divided into four categories depending upon the predicted immigration from other units: stepping-stone sink, sink, itinerant, or unoccupied (see Table 1).

This geographic prediction of opossum distribution was compared with the locations of road-killed opossums along transects in the region (Kanda et al. 2006). We had previously developed a null model of points on these transects for comparison, where the points were drawn from a uniform spatial distribution but point selection was biased to reflect uneven observer effort (Kanda et al. 2006). We used logistic regression with population class coded in dummy variables to predict if a point was likely to be a kill.

Sample size caveat

We were confronted with relatively small sample sizes in attempting to assess reproduction, age-specific survival, and dispersal of this opossum population. We are

well aware of the risks attending calculations based on such limited data, but elected to proceed because so little is known about the dynamics of this species, especially at the edge of its geographic range, and better information will not likely be available in the near future. Sample sizes are given for all our calculations so that their merit can be judged independently by the reader.

RESULTS

Reproduction

In central Massachusetts, female opossums breed within the year after birth, producing large litters (9.8 ± 0.45 young [mean \pm SE], $n = 20$) with an even sex ratio (51% female, $P = 0.78$, $n = 115$, $\chi^2 = 0.078$). Based on 29 females, we estimated that the average 1-yr-old female produces 1.34 litters, or 6.74 female offspring (minimum-maximum estimates for the study were 1.03–1.55 litters producing 4.99–8.18 female offspring; for details see Kanda 2005b). The mean parturition date of 11 urban first litters was 11 March (± 8 days), whereas the mean parturition date of 11 first litters in natural habitats was significantly later, occurring on 9 April (± 5 days) (two-tailed t test equal variance, $P = 0.004$, $t = 3.259$). Only urban females showed evidence of two litters. We had little data for older (2-yr-old) females, so we used the litter size and sex ratio from 1-yr-old females for both age classes in the life-table model.

Young-of-year survival

Survival of young-of-year was high both in pouch (minimum number alive, 0.935, $n = 46$) and during weaning (Cormack-Jolly-Seber [CJS], 0.847 ± 0.250 , $n = 65$). Survival then declined during the first four weeks of independence (CJS, 0.583 ± 0.287 , $n = 38$), for a total survival rate of 0.462 for young over the breeding period (Fig. 2). Thirty young-of-year (nine male, 21 female)

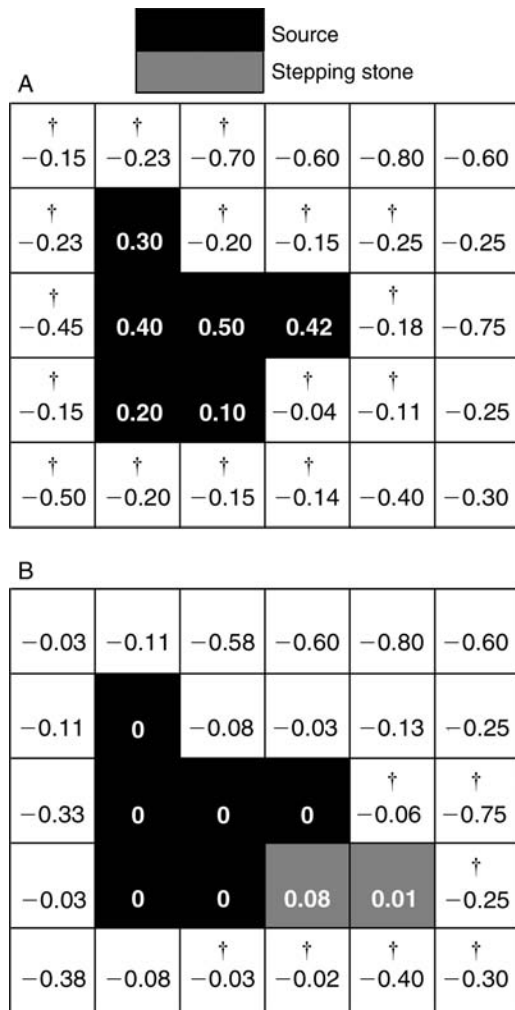


FIG. 1. Geographic modeling procedure. (A) Each unit begins with a value (K) based on the proportion of urban habitat within the unit. Those with positive K are designated "source"; adjacent non-source units are indicated with daggers (†). (B) K value for the contiguous source area (1.92) is distributed to the 16 adjacent units ($1.92/16 = 0.12$ added to each unit). Units that have changed to a positive K are designated stepping-stone sinks. K value from these stepping stones will be redistributed to the next adjacent units.

were radio-collared in autumn. We observed no effect of sex on persistence, dispersal, or cause-specific mortality rates (Cox proportional hazards regression, all $P > 0.98$, $\chi^2 = 0.000$), so males were included in estimates of young-of-year autumn rates. Point estimates of autumn survival rates of young opossums in the two habitats were similar in urban and natural habitats (Table 2), however the majority of deaths in the natural habitat were due to predation while the majority in urban habitat were from vehicles (Table 3).

No monitored subadult females persisted until spring in natural areas (Table 2). Subadult female opossums over-wintering in natural habitats were 12.8 times as likely to die of starvation as subadult females in urban

habitats (Cox, $P = 0.020$, $\chi^2 = 5.384$). Of three urban animals that starved (2 female and 1 male subadults), two were raised in natural habitat, while the third's origin was unknown. Taking into account animals of unknown fate, the persistence rate estimates were 0.074 (95% CI 0.012–0.444) in natural and 0.697 (95% CI 0.422–1.000) in urban habitats.

Subadult female mass

Size of young females entering winter differed by habitat, although this difference was due to age, not growth rate (see Kanda 2005b). In urban areas, subadult females in late autumn averaged 2.43 ± 0.11 kg and 235 ± 16 days old ($n = 5$), while those from natural habitats averaged 1.92 ± 0.12 kg and 206 ± 6 days old ($n = 8$). Juvenile female opossums from urban habitats were heavier (two-tailed t test equal variance, $P = 0.016$, $t = 2.845$) and older (two-tailed t test equal variance, $P = 0.035$, $t = 2.399$) than females from natural habitats.

Adult survival and movement

In spring, adult females may disperse to a new range (Table 3). Of nine 1-yr-old females tagged in urban habitat in the spring, one dispersed to a natural area before raising her litter (dispersal rate 0.079 ± 0.075 [mean \pm SD]). Two other urban females, and three of four females in natural areas, were originally captured during spring dispersal movements, so their wintering habitat was unknown.

All females that survived weaning of their first litter subsequently shifted to new ranges. All females already in urban habitat remained urban. However, females from natural habitat began using anthropogenic resources when they left their breeding range; no adult females persisted into winter in natural areas. Between April and November, adult females were 15.2 times as likely to move from natural to urban areas than vice versa (Cox, $P = 0.017$, $\chi^2 = 5.733$).

Adult females in urban areas did not appear to be subject to over-winter starvation (Table 2). Because of non-weather related deaths, the point estimate of winter persistence for urban adult females (0.615; 95% CI = 0.313–1.000) appeared similar to that of their younger urban counterparts. We observed five 2-yr-olds, but saw no opossums ≥ 3 yr old. We assumed there is no survival to 3 years, as generally found elsewhere (Gardner and Sunquist 2003).

Life-table model

A closed two-population life-table model stabilized after iteration with a total per capita population growth rate (λ) of 1.26 (Fig. 2). A second model using bias-adjusted persistence rates also yielded a growing total population ($\lambda = 1.19$). In Monte Carlo simulations with stochastically generated parameters, the model had a mean λ of 0.99 (95% CI = 0.24–2.81), or 0.95 (95% CI = 0.22–2.75) with bias-adjusted point estimates. Monte Carlo simulations with parameter variation restricted by

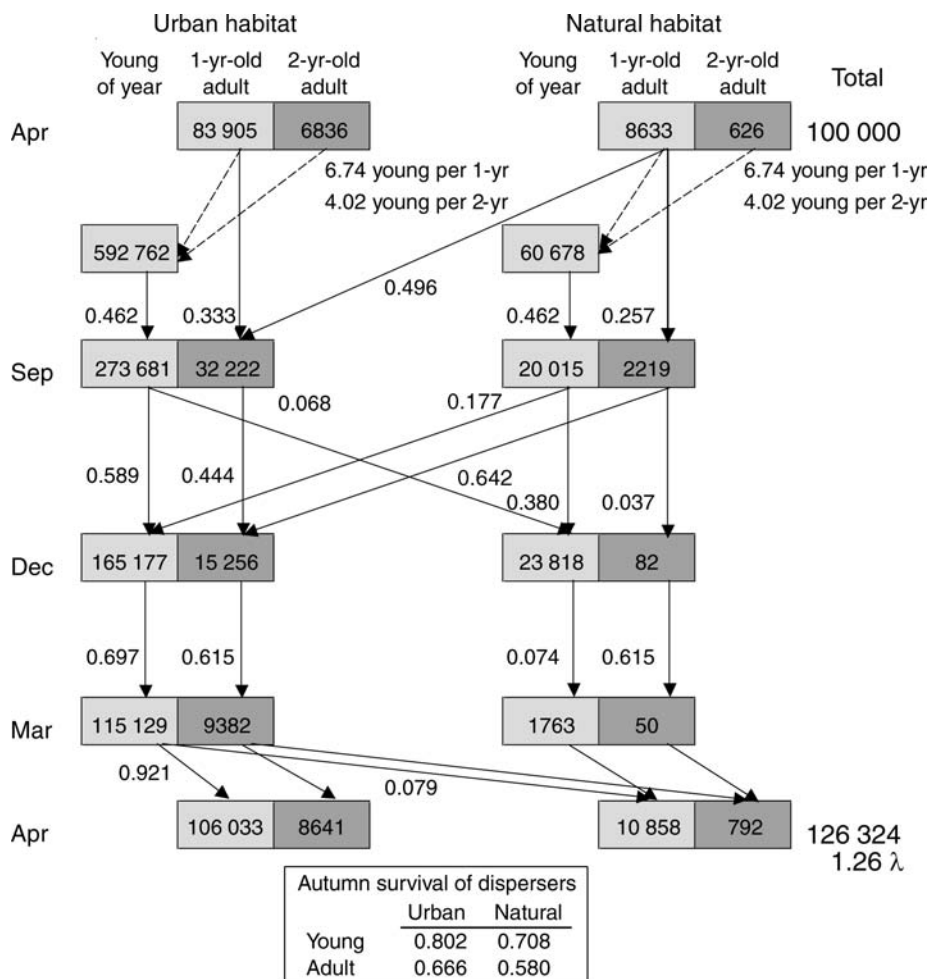


FIG. 2. Flow chart of the stabilized life-table model with two interacting populations of Virginia opossums (*Didelphis virginiana*), using the original point estimates of reproduction, persistence, and dispersal. Post-breeding survival of 2-yr-old females is assumed to be 0. Each box contains the theoretical number of females in a cohort at a given time of year. Numbers on the right are the totals for both habitats in April and the calculated population growth over one year.

TABLE 2. Seasonal persistence and habitat-specific survival rates for Virginia opossums (*Didelphis virginiana*) in central Massachusetts, USA, by age and habitat, with associated 95% confidence intervals.

Age, by season	Habitat	N	Radio days	Persistence	Sample size bias-adjusted persistence	Survival
Breeding (15 April–30 August)						
1 yr	urban	19	1014	0.290 (0.129–0.649)	0.265	0.333 (0.155–0.712)
1 yr	natural	5	308	0.257 (0.055–1.000)	0.178	0.636 (0.262–1.000)
Autumn (1 September–30 November)						
YOY	urban	19	1036	0.589 (0.386–0.899)	0.576	0.644 (0.437–0.946)
YOY	natural	14	661	0.380 (0.185–0.776)	0.354	0.501 (0.273–0.916)
1 yr	urban	12	676	0.444 (0.232–0.848)	0.420	
1 yr	natural	3	84	0.037 (0.001–1.000)	0.000	0.336 (0.039–1.000)
Winter (1 December–14 April)						
YOY	urban	8	748	0.697 (0.422–1.000)	0.674	
YOY	natural	9	419	0.074 (0.012–0.444)	0.043	
1 yr	urban	6	557	0.615 (0.313–1.000)	0.579	
1 yr	natural	0	0			

Note: Young of year (YOY) autumn rates include males; all other rates are only females. N is number of animals; radio days is the number of days these animal were tracked, collectively. See *Methods: Parameter analysis* for explanation of persistence and bias-adjusted persistence.

TABLE 3. Seasonal dispersal and cause-specific mortality rates for Virginia opossums in central Massachusetts by age and habitat, with associated 95% confidence intervals.

Age, by season	Habitat	<i>N</i>	Radio days	Dispersal	Starvation	Predation
Breeding (15 April–30 August)						
1 yr	urban	19	1014	0.079 (0.000–0.227)		0.079 (0.000–0.227)
1 yr	natural	5	308	0.496 (0.020–0.972)		
Autumn (1 September–30 November)						
YOY	urban	19	1036	0.068 (0.000–0.198)		
YOY	natural	14	661	0.177 (0.000–0.399)		0.355 (0.079–0.630)
1 yr	urban	12	676			0.185 (0.000–0.416)
1 yr	natural	3	84	0.642 (0.120–1.000)		
Winter (1 December–14 April)						
YOY	urban	8	748		0.303 (0.000–0.652)	
YOY	natural	9	419		0.694 (0.399–0.990)	
1 yr	urban	6	557			
1 yr	natural	0	0			

Note: Young of year (YOY) autumn rate includes males; all other rates are only females.

† Individual died of parasite load.

‡ Bulldozer buried den.

literature estimates had an average λ of 1.29 (95% CI = 0.55–2.62).

In the original Monte Carlo simulations, uncertainty in the independence period survival rate explained 49.7% of the variation in the population growth rate (Table 4). The other rates contributing to the calculation of young-of-year survival in urban areas (survival rates for weaning, urban subadult autumn, and urban subadult winter) each explained 10–13% of the population growth rate variability. All the remaining parameters had little influence on the changes in population growth rate. In contrast, in the sensitivity analyses, λ was sensitive to the reproductive output of 1-yr-old females as well as the survival of urban young-of-year. Altering the sex ratio of litters would have the largest impact on population growth rate (changing over 0.21 if proportion of females changes 10%; Table 4).

Geographic model

Five female opossums that were monitored while raising first litters on anthropogenic resources used an average of 9.9 ± 1.2 ha. The breeding ranges of four females in natural habitat were more variable and

tended to be larger (20.7 ± 5.2 ha). During the breeding season, opossums are aggressive against the same sex (Gardner and Sunquist 2003), so we assumed that a saturated urban habitat would have 10 females/km² and a saturated natural habitat would have 5 females/km². The life-table model suggested 10 urban female opossums and one natural habitat female together could replace themselves and generate an additional 2.9 females that may emigrate to new territories. In geographic terms, 10 females occupy 1 km² of urban habitat and would support a 0.2-km² sink of one female attempting to breed in natural habitat. The reproductive efforts of these 11 females would together produce 13.9 females for the following year (at $\lambda = 1.26$), 2.9 of which must locate unoccupied habitat in the next year. If all urban habitat is already filled, then these 2.9 emigrants must use surrounding unoccupied natural area (an additional 0.58 km²) that will act as an unproductive sink. Thus, we expect opossums in 1 km² of urban habitat would form a stable total population with opossums in 0.78 km² of natural habitat. The bias-adjusted life-table model ratio of established urban and natural habitat remains 10:1, but only 2.1 additional

TABLE 4. Demographic parameters having the largest influence on total population growth rate.

Parameter	Estimate	95% CI	Partial r^2	Stochastic $\delta\lambda$ †	Static $\delta\lambda$ †
Independence survival	0.583	0.020–1.000	0.497	0.17	0.20
Weaning survival	0.847	0.357–1.000	0.128	0.13	0.14
Urban subadult winter survival	0.697	0.422–1.000	0.123	0.14	0.17
Urban subadult autumn persistence	0.589	0.386–0.899	0.105	0.15	0.20
Litters per 1-yr-old female	1.34	1.03–1.55	0.024	0.09	0.08
Litter percentage female	0.51	0.43–0.60	0.016	0.21	0.24
Litter size	9.80	8.92–10.68	0.004	0.10	0.12
Pouch survival	0.935	na	na	0.11	0.12

Notes: Partial r^2 is the proportion of the variance in λ from the original Monte Carlo simulations attributable to variation in the parameter; $\delta\lambda$ is the sensitivity of population growth rate to the parameter using the stochastic and static methods. All other parameters had partial $r^2 < 0.01$ and both measures of sensitivity < 0.05 ; na, data not available.

† Per 10% change in parameter (0.10 in rates; 10% change in litter size = 1 young).

TABLE 3. Extended.

Road	Other or unknown
0.474 (0.205–0.742) 0.248 (0.000–0.666)	0.079 (0.000–0.227)
0.205 (0.000–0.411) 0.278 (0.013–0.543)	0.137 (0.000–0.313) 0.089 (0.000–0.254) 0.093† (0.000–0.265)
0.321 (0.000–0.837)	
0.116 (0.000–0.329) 0.192 (0.000–0.530)	0.116 (0.000–0.329) 0.192‡ (0.000–0.530)

emigrant females would be produced, occupying on average 0.42 km², for a total natural habitat sink of 0.66 km². For simplicity, we rounded to a conservative 0.5 km² of natural habitat supported by each 1 km² of urban habitat ($r = 0.5$).

Of 5755 km² in the Connecticut River Valley, 823 km², or 14.3% of the landscape, was modeled as source for opossums at the 1-km² scale (Fig. 3A). These sources were surrounded by 2085 km² of occupied sink areas. At least two adult female opossums were predicted to be breeding in these sinks year after year; however, these areas would rely upon immigrants to annually replenish the population. Of the sink area, 461 km² were classified as stepping-stone sinks, meaning that although the unit population would decline without immigrants, with the predicted spring influx of females the unit would produce emigrants in the fall. A total of 50.5% of the valley was predicted to have opossums (source or sink). All remaining units were within 10 km of a population, making them “itinerant” territory: occasional dispersers could appear but breeding would not regularly occur. The distribution of 157 road-killed opossums recorded in the Connecticut River Valley (Kanda et al. 2006, Fig. 3B) was consistent with predictions from this geographic model (Table 5). The odds of a transect point being a kill over a null model point were highest in source areas and lowest in itinerant areas.

DISCUSSION

Virginia opossum population dynamics

Virginia opossums in central Massachusetts appear to rely upon anthropogenic resources for winter survival, creating a seasonal source-sink dynamic between urbanized and natural habitats in the region. The two habitats seem to be of similar quality in warm months, but during winter the resources provided in human-dominated landscapes have a critical positive influence on survival rates of subadult females.

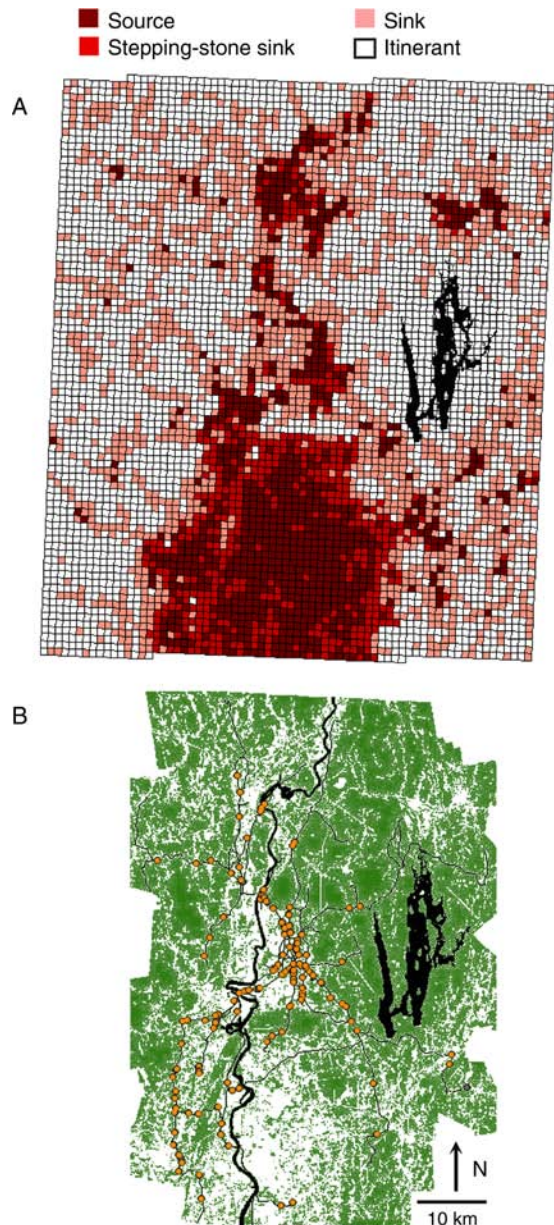


FIG. 3. (A) Predicted distribution of opossum source and sink populations by square kilometer in central Massachusetts, USA, west of Quabbin Reservoir (black) and (B) the distribution of road-killed opossums (orange circles) on road transects monitored in the region in 2000 and 2001, with the background denoting forest (green) and urban (white) habitat, from Kanda et al. (2006).

Young-of-year female opossums that survived the winter lived in human-dominated areas and entered winter older and larger than young females in natural areas (see Plate 1). Previous energetic modeling suggests that subadult females need to reach 2.5 kg by 1 December to survive winter temperatures found in central Massachusetts (Kanda 2005a). We found that females raised in urban habitats attained this mass.

TABLE 5. Logistic regression prediction of whether a transect point is a kill (1) or null model point (0) based upon the geographic population model.

Parameter	Estimate	SE	Wald χ^2	P	Odds ratio	Odds ratio 95% CI
Constant	-0.961	0.362	7.040	0.008		
Source	1.194	0.323	13.656	0.000	10.885	3.068–38.614
Stepping stone	0.951	0.333	8.169	0.004	6.701	1.818–24.696
Sink	0.661	0.330	4.012	0.045	3.750	1.029–13.671

Note: Population classes were coded with dummy variables, with itinerant class as the base uncoded category.

Litters raised in urban habitats were born a month earlier on average than litters in surrounding natural habitats, giving offspring more time to grow and store fat reserves for winter. Because females in urban areas raised their first litters earlier than females in natural habitats, they were the only ones observed to raise second litters. Judging from the size of some animals caught in urban areas during spring, we suspect underweight females (second litter or raised in natural areas) may also be able to survive winters if they can access anthropogenic resources such as garbage and outdoor pet food.

The total population growth rate is highly sensitive to eight parameters related to the birth and first-year survival of urban young. Yet of these, the three parameters defining reproductive output of 1-yr-old females account for little of the simulated variation in population growth rate because we have high confidence in these estimates for this study period. Spatiotemporal stochastic variation in these parameters could have a strong influence on population growth, however there is no indication either within our study or in comparison to other studies to suggest that population reproduction is highly variable. Litter sex ratio, in particular, has the potential to strongly influence population growth, however opossum populations rarely deviate far from the even litter sex ratio seen here (Gardner and Sunquist 2003). Litter sizes gradually increase and number of litters gradually decreases with latitude (Kanda and Fuller 2004). Our estimates of the litter size and number of litters per female are consistent with previous findings from nearby New York (litter size 9.4, 1.25 litters/female; Hossler et al. 1994). There is little further room for litter sizes to increase, as the maximum litter is capped at 13 by the number of nipples. On the other hand, litter size and number of litters could be restrained by energy limitation, but this is far more likely to influence natural than urban habitat animals.

While the survival of young in pouch is also clearly important in this life cycle, we unfortunately do not have a variability estimate for this parameter. From the literature, we see that in-pouch survival is consistently very high in opossums throughout their range (Kanda and Fuller 2004). This indicates that, like reproduction, although variation in in-pouch survival has the potential to greatly alter the population dynamics, there is little natural variation available.

In this study, half the simulated variation in the per capita growth rate came from large uncertainty in the survival rate estimate for the independence period. All told, uncertainty in the survival estimates of urban young between leaving the pouch and the next spring is responsible for the vast majority of simulated variability in population growth rate. Although the life-table model references 27 parameters, many of which have poor confidence intervals, the wide uncertainty in the resulting population growth rate is responding only to the estimations in survival of urban young-of-year. When young leave the pouch and begin to move on their own, during the weaning and independence periods, they are subject to increasing mortality. Our survival estimates for these periods are largely based on urban litters, and are slightly higher than have previously been recorded (Wright 1989, Hossler et al. 1994). Despite their importance, these estimates are also the least understood part of opossum life history. Predation is believed to be the primary cause of death for young opossums (Gardner and Sunquist 2003). However, urban predation rates were low for radio-tracked animals (older than first independence) suggesting that urban association may protect opossums from common predators such as coyotes (*Canis latrans*) and bobcats (*Lynx rufus*). Over the course of the study, we observed no juvenile opossums of weaning or first independence age dead on the roads. Without substantial predation or vehicle mortality evident, our high estimate of independence period survival seems reasonable for urban animals despite poor statistical confidence.

The large error estimates associated with many of our parameters are driven by small sample size, and are probably larger than the usual temporal process variation in these parameters. As noted above, in the crucial aspects of the life history our point estimates are sensible in the framework of what is known about opossum demographics. When we used this outside knowledge to restrict the uncertainty in the parameters, the average growth rate was consistent with the point-estimate model, and showed a growing population.

We have no data to extrapolate how population growth may change in this area over time, but we predict that in urban areas human presence should reduce temporal variation in life history parameters by providing consistent resources (food, shelter) and risks (mortality from vehicles) from year to year. Environ-



PLATE 1. A young Virginia opossum female, born in a natural habitat, reached first independence in mid-June. This late start made it unlikely for the female to survive the winter without locating anthropogenic resources. Photo credit: Kevin A. Kanda.

mental stochasticity would be expected to cause greater variation in life history parameters for natural habitat animals, particularly winter survival rate fluctuating strongly with winter climate. However, total population growth rate was not very sensitive to the fate of animals from natural habitats because few reproductive females were predicted to be produced in these areas. Occasional high survival of natural area young-of-year should increase the population growth rate; however, unless the offspring disperse to unoccupied urban habitat, the next year with restricted natural winter survival will cause a population decline (in the inflated natural population) and the population will shrink to its original distribution.

Virginia opossum distribution

In a source-sink dynamic, a substantial proportion of the total population may be found residing in marginal habitat that cannot provide the resources to maintain a species' life history (Pulliam 1988). This appears to be the case for the Virginia opossum in central Massachusetts. Although we expect greater density of opossums in source habitat because of smaller home range requirements, 72% of the predicted local distribution of opossums is in sink habitat at the 1-km² scale. At this scale, we expect opossum populations in a patchy distribution associated with, but not restricted to, highly localized anthropogenic resources.

Exploitation of anthropogenic resources can also explain the opossum distribution on a regional scale. In our model, we assumed that all urban areas were occupied. Extrapolating to the northernmost edge of the

species range, colonization of new urban habitat could occur each year as dispersers from occupied urban habitat locate new anthropogenic resources instead of being lost into unproductive natural habitat sinks. Females may move in the spring with young in pouch, and young move independently in autumn, with a maximum dispersal distance of about 10 km at each move (Gardner and Sunquist 2003), so opossums could expand their occupation of urban areas by up to 20 km a year, even if the intervening 20 km cannot support animals over winter. As opossums move farther north, a network of anthropogenic resources remains necessary to help females obtain sufficient mass and/or provision them over winter in colder regimes. Ultimately, opossum range expansion will be curtailed where subadult females cannot gain the energy reserves required to survive local winters even with available urban resources. Until that limit is reached, we expect Virginia opossums will continue to expand their populations northward coextensive with urbanized environments.

Source-sink range edge

With heterogeneous landscapes, one does not have to look at the extreme global geographic edge of the range in order to observe the active mechanism limiting the range. The Virginia opossum population we studied in Massachusetts is 200 km south of the northernmost reports of opossum distribution. Yet due to the mosaic landscape, the opossums in Massachusetts are also at the boundary of their realized niche.

Theoretical discussions suggest that declining habitat quality at the range margin result in declining fitness and

declining abundance in marginal populations (Guo et al. 2005, Holt et al. 2005) despite little empirical evidence (Sagarin et al. 2006). Considered as a single population (a more traditional approach), the average fitness and abundance at our study site would appear low, in keeping with this theory. However, rather than responding to a large-scale gradient of declining habitat suitability, opossum abundance forms a gradient at the landscape scale which overlays a sharp local dichotomy between suitable (urban) and unsuitable (natural) habitat.

It should come as no surprise that individual movement among these heterogeneous local areas plays a critical role in defining the local distributional edge. Consistent with metapopulation models (Lennon et al. 1997, Bahn et al. 2006), recent studies on such diverse organisms as intertidal limpets (Gilman 2006), the common sandpiper (Dougall et al. 2005), and monkeyflowers (Angert 2006) have found range edge populations with survival and breeding success equivalent to or higher than more central populations, leaving cross-population recruitment the pressure point for limiting mechanisms. Similarly, core urban populations of opossums in Massachusetts may have not only equivalent but higher fitness than many populations more central in the species' range. The local range edge is then defined by the annual redistribution of individuals into the natural landscape.

Because populations in the source habitat may support a larger geographic area of sink habitat, the majority of the regional distribution is sink habitat. Not all sink habitat is occupied, making an abundance gradient on the landscape where organisms are present in some natural areas and not in others because of differential immigration, not differential habitat suitability. The conservation implications are distressing; attempts to predict and manage species distributions could be grossly misdirected if they use occupancy to identify habitat requirements.

The influence of urbanization on opossums is a case of positive anthropogenic influence on species distribution, but a negative impact would also create a local source-sink dynamic. Human development is not spatially autocorrelated at the biogeographic scale of most species' ranges, although it does usually grade at the landscape scale (the urban-rural gradient). This makes human-dominated landscapes particularly important areas for looking at local scales to understand species distribution, although there is no reason that strong local heterogeneity resulting in source-sink dynamics would be limited to the case of anthropogenic influences.

Spatial scale is extremely important in considering populations and their dynamics, and populations at the species' distributional limit should be no exception. Our study demonstrates the importance of considering landscape-level effects of habitat heterogeneity on fitness parameters. Rapid environmental changes occurring on global and local scales provide both opportunity and urgency for the empirical examination of species'

distributional responses (Parmesan et al. 2005). Direct measurement of individual fitness can aid in estimating population growth rates while assessing the factors influencing specific survival and reproduction parameters. This approach allows the identification of source and sink populations that may not be easily delimited geographically.

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SUPPLEMENT

Monte Carlo simulation of the life tables of two interacting Virginia opossum populations (*Ecological Archives* E090-108-S1).