

## Winter energetics of Virginia opossums *Didelphis virginiana* and implications for the species' northern distributional limit

L. Leann Kanda

Kanda, L. L. 2005. Winter energetics of Virginia opossums *Didelphis virginiana* and implications for the species' northern distributional limit. – *Ecography* 28: 731–744.

While climatic limitations are widely recognized as primary factors determining the distributions of many species, the physiological link between climate and species' persistence is poorly understood. The Virginia opossum *Didelphis virginiana* is a species for which winter energetics have been evaluated and a northern geographical limit has been hypothesized. Expansion of opossum populations beyond this limit, however, suggests that a previous winter energetics model requires modification. I update this energetics model by incorporating random foraging success to estimate the probability of opossum survival under varying winter temperature regimes. Estimation of opossum "success" for winters in Amherst, Massachusetts, since 1926 showed that juvenile females, the key breeding component of the population, would survive at a rate high enough to maintain a stable population in only 4 of the 77 yr. The model correctly predicted the fate of 13 of 14 opossums monitored in the Amherst area during the winters of 2000–2003. The current energetics model does not correctly predict autumn weight gain, but it does accurately estimate opossum winter survival. However, the model predicts that opossums should be winter-limited in areas such as Amherst, Massachusetts, where in fact they are well established. This discrepancy may be explained in three ways: weather station data do not adequately reflect available microclimates, opossums show high levels of flexibility in cold-weather foraging behavior, and most likely, humans provide food and shelter that mitigate the effect of winter.

L. L. Kanda ([lkanda@bio.umass.edu](mailto:lkanda@bio.umass.edu)), Graduate Program in Organismic and Evolutionary Biology, 319 Morrill Science Center South, Univ. of Massachusetts, Amherst 01003, MA, USA.

Climatic factors have long been acknowledged as principal agents responsible for limiting the distributions of species (Wallace 1876, Rosenzweig 1995, McNab 2002). As humans modify local and global climates, understanding the mechanisms by which climate determines species' persistence is increasingly important (Humphries et al. 2002). In many cases, however, the implications of climate change for species' ranges are based upon broad correlations, and proximate mechanisms are rarely examined (Humphries et al. 2002, McNab 2002: Chapter 14).

The northern distribution of the Virginia opossum *Didelphis virginiana* is perhaps one of the best-studied

cases of mammalian range limitation by climate. A tropically evolved species, the opossum's distribution in North America has been expanding northward in historical times (Gardner and Sunquist 2003). Correlations have been reported between the opossum's northern range limit and the  $-7^{\circ}\text{C}$  January isotherm (Tyndale-Biscoe 1973), and northern animals have been observed with severely frostbitten tails and ears (Long and Copes 1968). At the northern edge of their distribution opossums have been found dead of starvation in early spring (Blair 1936), and a correlation of opossum sightings in Ontario with warm winters is suggestive of climatic limitations (Peterson and Downing 1956,

Accepted 2 May 2005

Copyright © ECOGRAPHY 2005  
ISSN 0906-7590

de Vos 1964). The winter energetics of opossums have been examined in the laboratory (Brocke 1970, Pippitt 1976, Hsu et al. 1988); these studies indicate that opossums have poor thermoregulatory ability in cold weather, poor fur insulation, and that they reduce the effect of cold winters primarily through behavioral avoidance. For example, opossums do not forage on nights below ca  $-4^{\circ}\text{C}$  (Wiseman and Hendrickson 1950, Brocke 1970). Brocke (1970) used energetic parameters obtained in the laboratory to estimate the physiological limitation of opossums, then linked this estimation with climatic data to hypothesize that the Virginia opossum was at or close to its potential northern distribution in central and northeastern North America.

The current distribution of the opossum casts doubt on the predicted winter physiological limit. Opossums have expanded their range into areas where it was believed they could not survive. The most generous distributional estimate given by Brocke (1970) suggested opossums could survive as far north as mid-Vermont and New Hampshire. However, opossums currently are reported throughout these states and into Canada (Gardner and Sunquist 2003).

Given this contradiction in the expected and actual distributions of opossums, I re-examined Brocke's (1970) energetic model to determine if any of its assumptions or limitations reduce its applicability to northern opossum population persistence. I modified the energetic parameters to form an updated model, and applied this model to the Amherst, Massachusetts, region. According to all previous studies (Brocke 1970, Tyndale-Biscoe 1973, Pippitt 1976, Gardner 1982) Massachusetts should fall within the physiological distributional limit of Virginia opossums, and they first appeared in the state in the early 1920s (Gardner and Sunquist 2003). However, recent road-kill and camera surveys indicate opossums are not present in central Massachusetts forests outside of the urbanized landscape, suggesting that the urban-rural interface in Massachusetts is a distributional edge (Kanda 2005). The new energetics model described in this paper predicts the fate of opossums given a range of pre-winter weights, success in foraging, and actual climatic data from Amherst, Massachusetts over the last 77 yr. I then tested the model using data from 14 winter-monitored opossums living in Amherst.

### Brocke's (1970) energetic model

The most detailed winter energetic parameters available for the Virginia opossum come from Brocke's (1970) dissertation on animals from a Michigan population. He estimated the energy intake and energy expenditure of opossums under two scenarios: days in which opossums leave their den to forage, and days in which opossums

remain in their dens. For each scenario, Brocke estimated the energy intake and energy expenditure of captive animals in outdoor pens. For energy intake if the animal forages, Brocke measured the energy in daily ad libitum intake of opossums feeding on carrion. For energy expenditure, he measured weight loss of captive animals over periods when they chose to be "highly active" (i.e., foraging) and periods when they remained inactive in their dens. Brocke used observed weight loss in captive animals, as well as condition of roadkill carcasses throughout the winter, to estimate that the average opossum could lose up to 42% of its pre-winter body mass before starving to death. Because opossums catabolize muscle as well as fat reserves, Brocke measured that the opossum converts one gram of body mass to 4.4 kcal of energy ( $E_W = 4400 \text{ kcal kg}^{-1}$ ).

Brocke's arrangement of the energetic equations is not immediately intuitive; here I rearrange them slightly for interpretation in general terms of energy input and energy expenditure (using Brocke's notations where applicable; for parameter definitions and specific measurements see Table 1). The total winter energy expenditure ( $E_T$ ) is the sum of energy expenditure on resting ( $D_S$ ) and foraging ( $D_F$ ) days over winter:

$$E_T = D_S E_S + D_F E_F$$

On foraging days the animal will add to its energy stores a daily intake  $E_I$ , so total energy gained overwinter from food ( $E_G$ ) is

$$E_G = D_F E_I$$

and therefore net energy loss ( $\Delta E$ ) overwinter is simply the difference,

$$\Delta E = E_T - E_G$$

The net energy lost overwinter comes from the opossum's body reserves ( $W$ ). The maximum net energy loss permissible before starvation occurs is therefore the energy obtainable from the reserve body mass

$$\Delta E_{\max} = W E_W$$

The maximum number of energy-expensive resting days an opossum can tolerate overwinter, then, is determined with substitution and rearrangement:

$$W E_W = E_T - E_G \quad W E_W = D_S E_S + D_F E_F - D_F E_I$$

$$D_S = \frac{W E_W + 120 (E_I - E_F)}{E_S + E_I - E_F}$$

Brocke concluded from captive and road-killed samples that the average pre-winter opossum ( $A_{(O)}$ ) weighed 3.04 kg. Based on his energetic measurements for an animal of this size (Table 1), Brocke calculated that a 3.04 kg opossum could theoretically survive up to  $DS = 90$  resting days, interspersed with 30 foraging days, if it eats ad libitum on the foraging days. Brocke also estimated that the average juvenile opossum would be

Table 1. Virginia opossum winter physiological parameters measured by Brocke (1970). Parameter names are mine, adapted from Brocke where possible.

Parameter	Measure	Description
$D_S$		Number of days in a 120-d winter spent resting in the den.
$D_F$	120- $D_S$	Number of days in a 120-d winter on which foraging occurs.
$E_s$		Energy spent during a resting day.
	$E_{S(O)}$ 113 kcal	Average opossum resting energy spent in 24 h.
	$E_{S(J)}$ 102 kcal	Juvenile resting energy spent in 24 h.
$E_F$		Energy spent during a foraging day.
	$E_{F(O)}$ 158 kcal	Average opossum foraging energy spent in 24 h.
	$E_{F(J)}$ 154 kcal	Juvenile foraging energy spent in 24 h.
$E_I$		Energy taken in from food on a foraging day.
	$E_{I(O)}$ 315 kcal	Ad libitum intake for the average opossum.
	$E_{I(J)}$ 270 kcal	Ad libitum intake for a juvenile opossum.
$L$		Ad libitum intake in 24 h by body weight.
$A$		Autumn opossum weight (1 December).
	$A_{(O)}$ 3.04 kg	Autumn average opossum weight.
	$A_{(J)}$ 2.59 kg	Autumn average juvenile weight.
	$A_{(FJ)}$ 2.37 kg	Autumn average juvenile female weight.
$P$		Percent acceptable weight loss.
$W$	$AP$	Mass of animal convertible to energy.
$E_w$		Opossum weight to energy conversion.

2.59 kg ( $A_{(J)}$ ) before winter, and could therefore lose 1.09 kg ( $W_{(J)}$ ). Brocke found that such smaller animals had slightly lower energy expenditure per day but could not eat as much ad libitum food as the average opossum (Table 1). Juvenile opossums should therefore be able to tolerate no more than 85 forced resting days in a 120-d winter.

What dictates the foraging behavior of an opossum in winter? Like Wiseman and Hendrickson (1950), Brocke had observed that winter opossum foraging activity is strongly linked to ambient temperature; opossums generally stop foraging if night temperatures are  $\leq -4^\circ\text{C}$ . (Pippitt [1976] found that opossums avoid foraging in temperatures much below  $0^\circ\text{C}$  because they lose thermoregulatory control in such temperatures.) Based upon daily temperature relationships in Lansing, Michigan, Brocke generalized that opossums would not forage if the daily maximum temperature did not rise above freezing.

In the end, Brocke realized that the opossum population should fail before reaching the conditions that restrict foraging to 30 d a winter, since ad libitum foraging in winter conditions is not realistic. He concluded that the average opossum should tolerate no more than 70 d of enforced resting in the den over winter, with 50 d of foraging. Though he built many models exploring opossum energetics when foraging fails to produce food, he had no empirical energetic evidence for this final decision. It was probably influenced by the fact that at the time the distributional limit of opossums in Michigan coincided with the isotherm of 70 d/winter with daily maximum temperatures below freezing. Brocke (1970) further generalized the geographical limitation as the southern edge of the pine-hemlock ecotone. These two estimates (the isotherm and the

ecotone) are typically quoted as the geographical limit imposed by the winter physiology of the opossum (Gardner 1982, Hsu et al. 1988, McNab 2002: Chapter 14, Gardner and Sunquist 2003).

## Methods

I formed a time-stepped computer model using MATLAB Student (Anon. 1997) that incorporated the energetic parameters measured by Brocke (1970) (Table 1). Instead of using the ratio of foraging to non-foraging days to estimate the theoretical range limit, I used weather station temperature data for winters in Amherst, Massachusetts (Northeast Regional Climate Center, Ithaca, NY and National Climatic Data Center, Asheville, NC) to estimate whether opossums would forage on a given day, and thus generated predictions of if and when an opossum would be expected to starve to death during an Amherst winter.

The model was constructed in a time-incremented fashion for two reasons. First, the order in which an opossum encounters enforced non-foraging days should be important (the animals may be able to survive a certain number of non-foraging days on average, but not if they all occur before the foraging days that replenish energy stores). Second, if animals are not eating ad libitum every foraging trip, the order in which they encounter more or less food in foraging bouts over winter could also be very important. This is also why the random foraging success model is stochastic; it allows the generation of a confidence interval on the model prediction of death date or weight of live animals in the spring, as well as weight of animals on any given date over winter.

The model requires input of the beginning opossum weight and a series of daily maximum temperatures representing a particular winter. In a loop procedure, each daily temperature was used to determine whether the opossum “foraged” or not. If the temperature was  $\geq 0^\circ\text{C}$ , the energy reserve parameter (the amount of body mass currently available before starvation) was increased by the net foraging gain; otherwise the resting expenditure was subtracted. If the energy reserve dropped to or below 0, the loop ended and the hypothetical opossum was considered dead; otherwise, the loop incremented to the next day.

### Perfect foraging juvenile simulation

I first constructed the model to simulate the ad libitum juvenile energetic model used by Brocke (1970). I began the model with the estimate of the autumn mean juvenile weight (Table 1), rather than the mean opossum weight, because juveniles are the most important age class for the upcoming breeding season. It is rare for an opossum to reach its second or third winter, as opossums are very short-lived for their size (Kanda and Fuller 2004). In the favorable climate of Florida, no more than 26% of 1-yr-old females lived to be 2 yr old (Sunquist and Eisenberg 1993). Farther north, Seidensticker et al. (1987) observed only 8% survival from 1 to 2 yr old in Virginia, and in Wisconsin no monitored females lived to their second breeding season (Gillette 1980). Given the apparent rarity of northern opossums successfully contributing to reproduction after their first breeding season (i.e. over-winter adults form a very small part of the subsequent breeding population), I considered juveniles to be the most important age class.

To replicate the ad libitum model in the time-stepped form, I set all the parameters to the energetic parameters measured and used by Brocke (1970) in his juvenile model (Table 1). I calculated mass changes of a hypothetical opossum that began with an input mean juvenile weight ( $A_{(J)} = 2.59$  kg), and which could lose 42% (P) of this weight before starvation (i.e.,  $W_{(J)} = A_{(J)}P = 1.09$  kg). Winter temperatures were defined in a matrix  $T_i$  where  $T_1$  is the maximum temperature ( $^\circ\text{C}$ ) from 1 December.  $W_i$  represents the body mass available for energy conversion on day  $i$  (i.e.,  $W_0 = W_{(J)}$ ). Days were incremented such that for  $i = 1$  to 120,

$$\begin{aligned} \text{if } T_i < 0, \quad W_i &= W_{i-1} - (E_{S(J)}/E_W) \\ \text{if } T_i \geq 0, \quad W_i &= W_{i-1} + [(E_{I(J)} - E_{F(J)})/E_W] \end{aligned}$$

until either  $i = 120$  or  $W \leq 0$ .

This simulation was run using temperature data from Amherst winters between December 1926 and March 2003. As it is a deterministic model, it was run only once for each winter data set. For each year, the expectation of whether the opossum would live or starve to death was recorded.

### Normally distributed foraging success model

Ad libitum foraging probably is unlikely during northern winters so I sought to simulate the random foraging success that an opossum is more likely to encounter in each foraging bout. Only anecdotal observations have been made of the forage available to opossums (a few direct observations or snow-tracks; Wiseman and Hendrickson 1950, Brocke 1970, Kanda unpubl.). Based on these anecdotes, I knew that in a winter landscape it would be possible for opossums to fail to find anything to eat during some foraging bouts. However, opossums also occasionally encountered sources such as carrion which were probably sufficient for ad libitum foraging opportunity. Finally, it seems reasonable that each of these scenarios is less likely than the opossum locating some intermediate amount of food (for example, insects burrowed in a log). I selected a model that required the simplest assumptions that would reflect this anecdotal observation of foraging success: a normal distribution where on average an opossum obtains 50% of its ad libitum intake.

I therefore modeled foraging success as a normal distribution with mean of 50% maximum ad libitum intake, and standard deviation of 25% of the maximum intake. I constrained the distribution between 0 and 131 kcal  $\text{kg}^{-1}$  of opossum. Brocke (1970) calculated 131 kcal  $\text{kg}^{-1}$  of opossum as the ad libitum intake; the constant figure of 270 kcal ( $E_{I(J)}$ ) represents 131 kcal  $\text{kg}^{-1} \times 2.06$  kg (mean mid-winter juvenile opossum weight). Because my model incorporates time, the current opossum weight reenters the calculation. Thus on any given foraging night, we generate success as  $S = (\text{random from normal distribution, } \mu = 65, \sigma = 33)$  kcal  $\text{kg}^{-1}$  opossum, and each foraging night recalculate energy intake as a function of success and current opossum weight:

$$E_{i,i} = S (A - W_0 + W_{i-1})$$

I ran each winter data set 1000 times, with foraging success selected randomly at each foraging bout within a run, and recorded the percentage of runs in which the opossum was expected to survive.

### Model parameter sensitivity

The energetic estimates used to parameterize the model do not include variability estimates. I preserved the deterministic nature of the energetic parameters in the normally distributed foraging success model and evaluated the model multiple times under differing values of each parameter. This approach allowed a clear interpretation of the magnitude of effect on survival per unit change in the parameters. I referred to data available in Brocke (1970) for estimation of appropriate value ranges. His study included both males and females, but he did

not indicate animal ages. I assume that animal weight influences energetic parameters, whereas age and sex do not.

Resting energy expenditure, foraging energy expenditure, the percentage of body weight available for energy conversion, and the critical foraging decision temperature were each varied in turn. Resting energy expenditure varied in Brocke's experimental animals between 1.44 and 2.36 kcal kg<sup>-1</sup> h<sup>-1</sup> per animal, which translates to 101–112 kcal d<sup>-1</sup> in 6 opossums weighing between 1.82 and 2.92 kg, and 141 kcal d<sup>-1</sup> for a larger 3.06 kg male (Brocke 1970: Chapter 8, Table 9). In the model, up to 10% variation from the original 102 kcal estimate is examined. Calculation from Brocke's (1970) table of energy requirements for higher activity periods (Chapter 8, Table 10) indicates a range of 129–206 kcal d<sup>-1</sup> in foraging energy for 8 animals. I examined the normally distributed foraging success model with foraging energy varying up to 20% from the original 154 kcal estimate (123.2–184.8 kcal). Four experimental animals monitored by Brocke (1970) for winter weight loss survived after 39.5 to 44.7% weight loss; interestingly the animal losing only 39.5% of its initial weight was noted to have almost died. A 5th animal did die after losing 42% of its initial weight. In the model, I varied the percentage of body weight available for energy consumption between 36 and 48% of the initial weight. Foraging occurred only at or above 0°C in the original model; I also examined the model when the foraging decision temperature was -2°, -1°, 1°, and 2°C. In each of these scenarios the number of foraging days was recorded.

The percentage of animals surviving the winter after 1000 runs of each scenario was compared to the null model (i.e., the original normally distributed foraging success model parameterized from Brocke's averages). For each scenario, years with 100% or 0% survival were ignored, as the difference from the null model is curtailed at the end of the probability distribution. The remaining data sets of change in survival probability by variant were analyzed in linear regression models using SAS ver.8 (Anon. 1999).

### Opossum autumn weight

The model has been evaluated with the beginning weight of the average juvenile (2.59 kg, as estimated by Brocke 1970). However, as opossums are polygynous and sexually dimorphic (with males larger than females), the critical group for over-winter survival is the female juveniles. From winter weights, Brocke back-calculated that female juveniles average 2.37 kg on 1 December (220 g lighter than the juvenile average). Therefore, I evaluated the model using beginning weights between 2.09 and 3.09 kg ( $\pm$  500 g), including 2.37 kg. As above, the model was run 1000 times for every beginning weight

and the percentage predicted to survive in each year was recorded. The change in probability of survival as the autumn weight differs from 2.59 kg was examined with linear regression (Anon. 1999).

### Verification of normally distributed foraging success model

During the winters of 2000, 2001, and 2002, I radio-collared opossums in the Amherst, Massachusetts, region. I captured opossums in wire cage traps in and around the Univ. of Massachusetts, Amherst campus. Animals were placed in a cloth bag and restrained by hand. Animals were weighed, sexed, aged via tooth eruption (Gardner 1982) and total, tail, hind foot, and ear lengths were measured. All female opossums received radio-collars (50 g), as did males if equipment was available. Radio-collared individuals were located via radio-telemetry once every 24–72 h. In warm weather, animals were recaptured once a month to adjust the collar fit and obtain the weight of the animal. The first winter, I attempted to recapture animals (#3 and #6); however, I immediately observed that I was actively disrupting their foraging opportunities with my capture attempts. Because I was concerned that such disruptions throughout winter could significantly reduce animal survival by reducing energy acquisition, I ceased my capture attempts (subsequent modeling showed that the few days I did potentially disrupt foraging were not sufficient to have altered the fate of these animals). In subsequent winters, animals were recaptured in warm spells, or not until spring. Radio-collars were equipped with mortality switches that altered the radio signal if the collar had not moved in 8 h. When animals died, every attempt was made to retrieve the body to determine death weight, condition, and cause of death. All capture and monitoring procedures were conducted in accordance with Univ. of Massachusetts, Amherst, IACUC protocol.

For the three years combined, 18 animals were monitored, beginning in December. Two were killed (roadkill and predation) before the end of the month, and two disappeared before spring. For the 14 remaining animals, both pre-winter weight (Table 2) and winter fate were known.

I assume that the energetic process described in the model is fundamentally the same regardless of animal age or sex per se, but instead depends upon the autumn weight of the animal (which is correlated with age and sex). Breeding begins late in the winter, but it is unclear whether males seek females (Ryser 1992) or vice versa (Pippitt 1976), so energetic demands of finding mates may not be sex biased. I therefore include all the animals for which I have winter data. In this sample, I have known survival outcomes of animals that began at

Table 2. Autumn and winter weights of opossums in the Amherst, Massachusetts, area monitored in the winters of 2000, 2001, or 2002.

Opossum	Sex	Age	Pre-winter		Mid-winter	
			Date	Weight (kg)	Date	Weight (kg)
3	F	J	3 Dec 2000	2.45	2 Feb 2001	1.31
6	F	J	6 Nov 2000	2.20	27 Jan 2001	1.45
22	F	A	11 Oct 2001	2.60	11 Jan 2002	3.16
27	F	J	15 Sept 2001	2.80	30 Jan 2002	3.35
28	F	A	20 Sept 2001	2.05		
63	M	J	17 Dec 2001	3.15		
74	M	J	27 Oct 2002	4.10		
80	F	J	11 Nov 2002	2.25	23 Dec 2002	2.00
82	M	J	20 Dec 2002	2.05		
86	F	J	16 Oct 2002	1.13		
88	F	J	5 Nov 2002	2.35		
89	F	J	9 Nov 2002	2.75		
92	M	J	20 Dec 2002	2.85		
100	M	J	20 Dec 2002	2.80		

particular autumn weights. I tested the model by simulating the winter for opossums at these weights and comparing model predictions with known fates of the animals. The normally distributed foraging success model was used with inputs to simulate each animal: the animal's pre-winter weight was used as beginning weight, and the first day of the temperature data was the date on which the pre-winter weight was taken. With 1000 runs of the model, the probability of survival for the animal was calculated. Either the date of expected starvation was recorded, or the expected spring weight of the animal, should it live. If an animal was caught and weighed mid-winter, the expected weight was also calculated from the model for the date in question.

To examine the effect of parameter variation on predictions of the normally distributed foraging success model, I altered the model with the high and low extremes previously examined for four parameters in the model (resting energy, foraging energy, percent weight loss, and foraging decision temperature). This resulted in 8 additional predictions of survival probability for each animal.

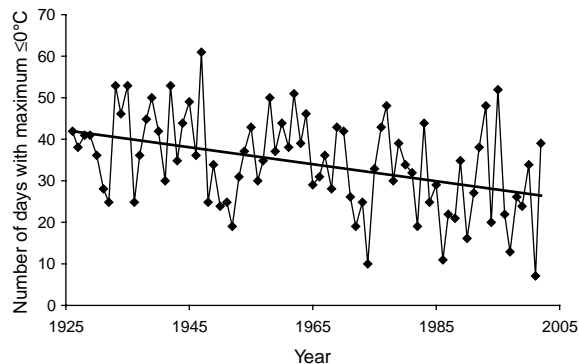


Fig. 1. The number of days between December and March with maximum temperature  $\leq 0^{\circ}\text{C}$  recorded at the local weather station for Amherst, Massachusetts, 1926–2002.

## Results

### Perfect foraging

Using the perfect foraging model, average-sized juvenile opossums would be expected to survive every Amherst winter from 1926 to 2002. The number of days in December through March with maximum temperature not exceeding freezing varied from 7 to 61 (Fig. 1). Over the last 77 yr, the number of winter days with maximum temperatures below  $0^{\circ}\text{C}$  declined (days below freezing =  $-0.2(\text{yr}) + 439$ ); however, only a small amount of variation in number of days below freezing was explained by year ( $r^2 = 0.16$ ). Juvenile opossums modeled with ad libitum intake on foraging days not only would be expected to survive all these Amherst winters, but to end March fatter than they were in December (Fig. 2).

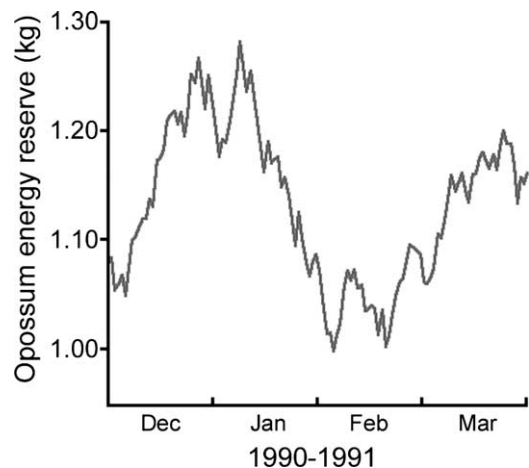


Fig. 2. Model output for perfect foraging success by juvenile opossums, for the winter of 1990–1991.

### Normally distributed foraging success

The survival prospects of juvenile opossums having random foraging success were considerably lower than the survival of opossums that ate ad libitum (Fig. 3a). In nearly half the years (35 of 77), <25% of average-sized juveniles would be expected to survive. For 17 of these years, the death toll from starvation was projected to be 100%. The probability of survival increased over the years (survival probability = 0.64(yr) - 1202), although year explained only a small amount of the variation in survival ( $r^2 = 0.14$ ). There are still years within the last decade with climatic regimes severe enough to predict no or low survival of opossums beginning winter at  $\leq 2.59$  kg.

### Model parameter sensitivity

Variation in each of the four parameters (resting energy expenditure, foraging energy expenditure, percentage of

body weight available for consumption, and foraging decision temperature) resulted in linear changes in average survival probability, as expected from the model structure. For any given year the effect of altered model parameters on survival probability would be difficult to predict, because the size of the effect was very different for different years. However, for each parameter the mean change in survival probability was strongly linear. For every kcal increase in resting energy expenditure, there was a mean reduction of 1.06% in survival (change in percent survival =  $-1.06(\text{resting energy}) + 107.97$ ;  $r^2 = 0.70$ ). Foraging energy expenditure had a larger effect, with an average decrease of 2.67% in survival for each additional kcal expended (change in percent survival =  $-2.67(\text{foraging energy}) + 406.20$ ;  $r^2 = 0.89$ ). The larger the percentage of the body weight that could be utilized as energy, the higher the probability of opossum survival (change in percent survival =  $1.71(\text{percent weight loss}) - 72.31$ ;  $r^2 = 0.73$ ). A shift in the foraging decision temperature had a large effect on

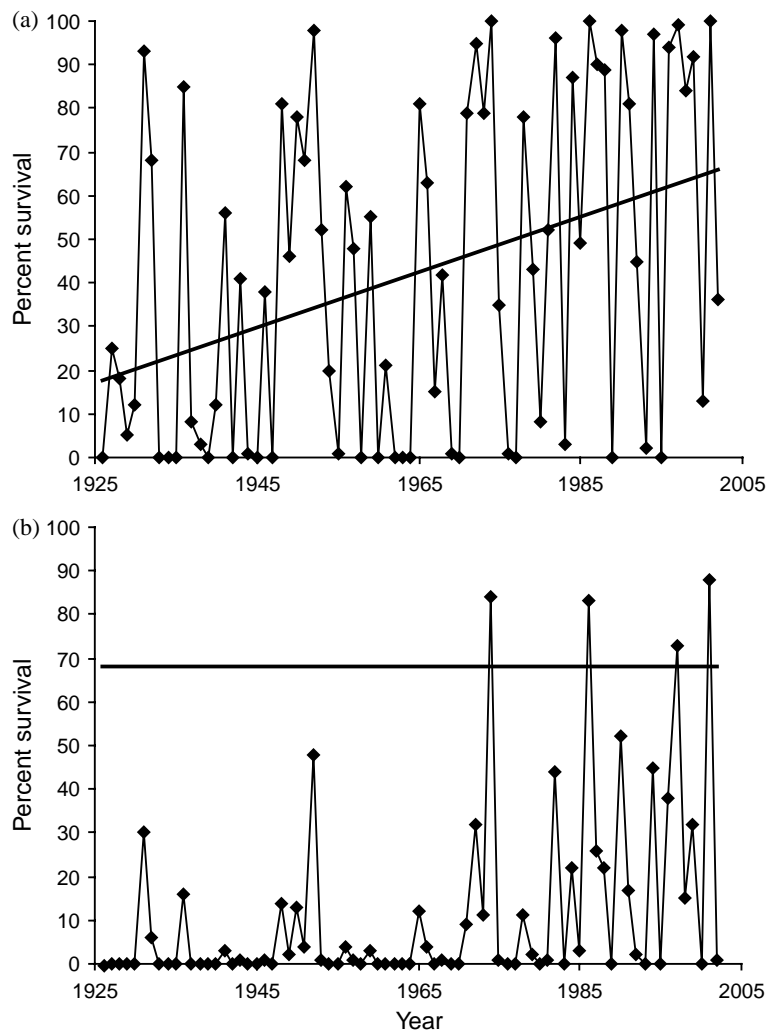


Fig. 3. The over-winter percent survival of (a) juvenile (2.59 kg) opossums and (b) female juvenile (2.37 kg) opossums predicted by a normally distributed random foraging success model under Amherst, Massachusetts temperature regimes.  $\geq 67\%$  survival of the female juveniles is estimated as necessary for opossum population persistence.

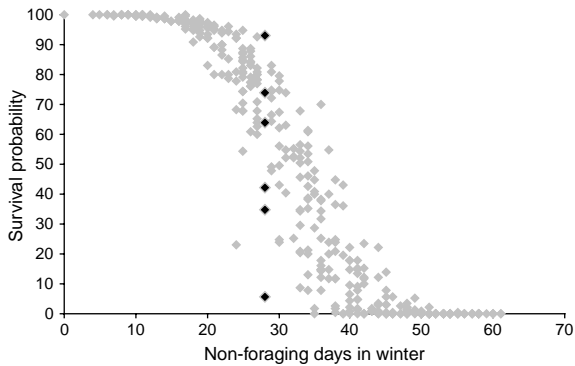


Fig. 4. The survival probability for a 2.59 kg opossum under different numbers of non-foraging days (produced through combinations of years and foraging decision temperatures). The range of survival probabilities possible under 28 non-foraging days is highlighted.

survival probability; a change in minimum foraging temperature of 1°C yielded a change in survival probability of 21.5% (change in percent survival =  $-21.52(\text{decision temperature}) + 1.5$ ;  $r^2 = 0.72$ ). The number of non-foraging days in a given year is determined by the minimum foraging temperature and the winter temperature regime. Because the order of non-foraging days is important, and is unique to each year, the predicted survival probability for a particular number of non-foraging days can vary widely (Fig. 4). For example, foraging temperature-winter regime combinations resulting in 28 non-foraging days had survival probabilities that ranged from 6 to 93%.

### Opossum autumn weight

An opossum's initial weight had a considerable effect on its survival probability (change in percent survival =  $200.8(\text{opossum kg}) - 525.6$ ;  $r^2 = 0.91$ ) (Fig. 5). A 25-g change in the opossum weight changed the survival probability by 5%.

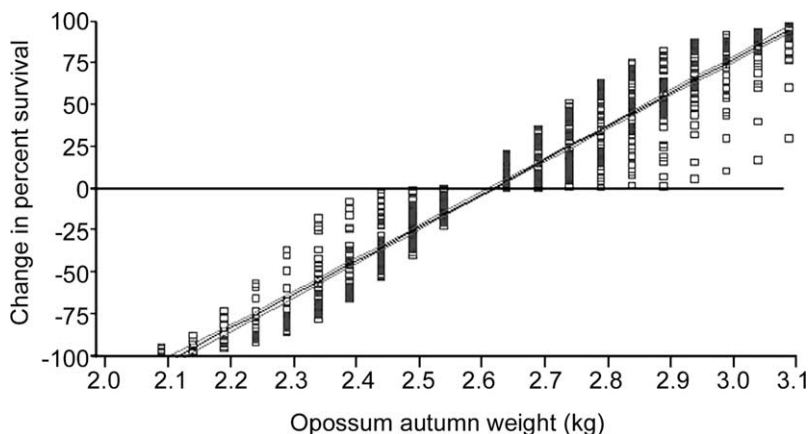


Fig. 5. Linear regression with 95% confidence intervals of change in survival probability as input weight is altered from the null weight of 2.59 kg.

If an average female juvenile begins winter at 2.37 kg, the model predicted a low probability of survival in most years (Fig. 3b). Fewer than 25% of females were expected to survive the winter in 64 of the 77 yr. For 35 of these 64 yr the model predicted that no 2.37 kg female could survive the winter. Because of limited reproduction (Hossler et al. 1994) and high mortality the rest of the year (Wright 1989, Sunquist and Eisenberg 1993, Hossler et al. 1994), Kanda and Fuller (2004) estimated that at least 67% of overwintering juvenile females need to survive in order to maintain a stable population. In contrast, the model shows only four years (1974, 1986, 1997, and 2001) in which at least 67% of the 2.37 kg females would be expected to survive.

### Model verification

Of the 14 live opossums for which I had over-winter data, the fates of 13 of the animals were correctly predicted by the normally distributed foraging success model (Table 3). In winter 2000, two juvenile females (#3 and #6) that were predicted to starve in early February did so, and their weights at starvation were within 110 g of the weight expected after a 42% reduction from their autumn weight (Fig. 6).

The winter of 2001 was particularly warm, and none of the three monitored animals died of starvation. The model correctly predicted survival for two of the three females (Table 3). Of the two females correctly predicted to survive, the mid-winter and spring weights of one female were correctly predicted (#22), while the other female's weights were greatly overestimated in the model (#27; 95% CI 3.57–7.29 kg midwinter instead of 3.35 kg, and 4.81–13.68 kg in spring instead of 3.30 kg) (Fig. 7). The third female (#28) was weighed early in the autumn and never recaptured, though she survived the winter. The model predicted that she should not survive the winter.



Table 3. Comparison of predicted and actual opossum fates. Predicted starvation weight is a deterministic 42% of the animal's autumn weight.

Opossum	Fate		Death date		End weight (kg)		
	Predicted survival probability	Actual	Predicted (95% CI)	Actual	Predicted (95% CI)	Actual <sup>a</sup>	%Δ
3	0.00	Starve	21 Feb (1 Feb–11 Mar)	7 Feb	1.42	1.31	-7.7
6	0.00	Starve	24 Jan (6 Jan–10 Feb)	5 Feb	1.28	1.23	-3.9
22	0.99	Lived <sup>b</sup>			4.59 (2.06–7.12)	2.75	-40.1
27	1.00	Lived			9.26 (4.84–13.68)	3.30	-64.4
28	0.00	Lived	20 Dec (16 Nov–22 Jan)		1.19	n/a	
63	1.00	Lived <sup>b</sup>			3.65 (2.65–4.65)	2.05	-43.8
74	1.00	Lived			10.35 (7.94–12.76)	2.8	-72.9
80	0.00	Starve	13 Feb (22 Jan–6 Mar)	17 Jan	1.30	n/a	
82	0.00	Starve	12 Mar (19 Feb–2 Apr)	25 Feb	1.19	1.05	-11.8
86	0.00	Starve	8 Nov (4 Nov–11 Nov)	28 Feb	0.66	1.02	54.5
88	0.06	Starve	23 Feb (26 Jan–22 Mar)	27 Jan	1.36	n/a	
89	0.93	Lived			2.45 (1.64–3.26)	1.75	-28.6
92	0.98	Lived			2.18 (1.67–2.69)	n/a	
100	0.94	Lived			2.05 (1.60–2.50)	2.25	9.8

<sup>a</sup> #28 and #92 lived but were not recaptured in the spring; the bodies of #80 and #88 were not retrievable but circumstances indicated death by starvation.

<sup>b</sup> #22 and #63 died on 21 Feb and 22 Mar, respectively, from non-winter related causes.

In 2003, all four smaller animals (females #80, #86, and #88, and male #82) had high model probabilities of starvation, and all died (Table 3). Animals #88 and #82 died in late January and late February, respectively, as predicted. Animal #82 was able to deplete his body stores by 140 g more than anticipated by the model before he died (Fig. 8). Animal #80 died a few days earlier than expected by the model, and although death weight was not obtained, her mid-winter weight was correctly predicted. Like #28, #86 was weighed early in the autumn. While she did die as predicted, she did not do so until February rather than November, and at death she weighed considerably more than the predicted 0.66 kg (Fig. 8).

The larger animals monitored in 2003 (males #63, #74, #92, #100, and female #89) all survived the winter, as expected (Table 3). The model suggested large weight gains for #74, inconsistent with an eventual weight in late April of 2.80 kg. Animal #63 was killed at the end of March and weighed 2.05 kg, slightly lower than the model's estimates of his spring weight. Spring weights of both #89 (Fig. 8) and #100 were consistent with the model.

### Predictions under parameter variability

No model with altered parameter estimates consistently predicted actual animal fates better than the null model (Table 4a). The one animal for which the null model failed to correctly predict its fate (#28) was correctly predicted to live only by a model with low foraging energy expenditure. Across all 14 animals, however, the low-foraging-energy variant correctly predicted the fates of only 10 of the animals. Alteration of the model to a high-foraging-energy variant or a 2°C change in either

direction in the foraging decision temperature also resulted in models with reduced predictive capability for these animals. Resting foraging energy or acceptable percentage of weight lost could both be altered from the null model without influencing the model's fate predictions. For animals that died, the null model correctly predicted the date of death in 4 of the 6 cases. Of the 7 animals that lived and were weighed in spring, the null model correctly predicted 3 weights. No model variant increased the accuracy of predicting the death dates of animals that starved or live weight of animals that survived (Table 4b).

### Discussion

While Amherst, MA, winters within the last three-quarters of a century are increasingly amenable to survival of small opossums, the model developed here suggests that most Amherst winters are still too cold to support a stable opossum population. The first records of opossums in Massachusetts date from the early 1920s (Gardner and Sunquist 2003); however, weather records for the late 1920s would predict low juvenile opossum survival (2.59 kg; <25%) and no survival of females averaging 2.37 kg. The large number of years in the 1970–2002 interval that should have permitted survival of young (2.59 kg) opossums cannot explain the previous establishment of opossums in the area.

Sensitivity of the normally distributed foraging success model to variations in the parameterization of the model depended greatly on the year. Averaged across years, the model was not very sensitive to changes in resting energy or acceptable percentage weight loss. The model results change more dramatically with foraging energy.

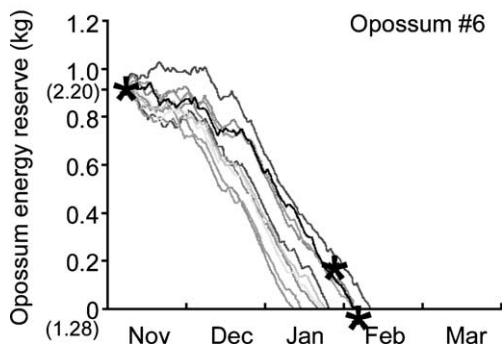
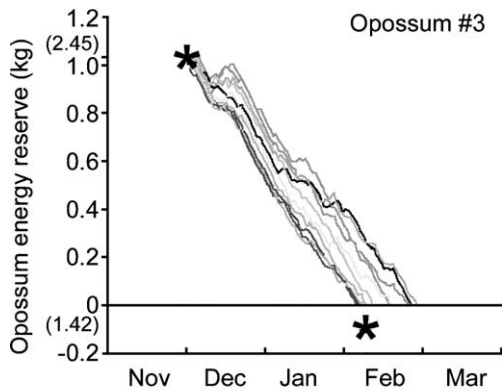
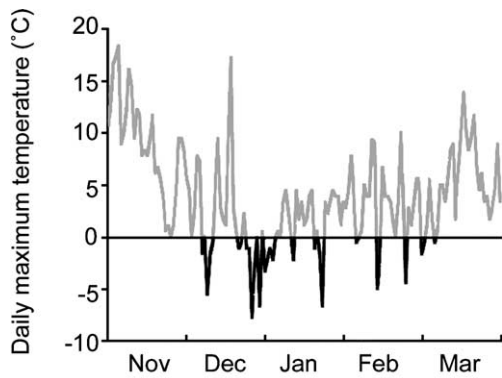


Fig. 6. Model output for simulation of animals #3 and #6, and the maximum daily temperatures recorded in the winter of 2000. For clarity, only 10 of the 1000 model runs for each animal is illustrated. \* denotes measured animal weights, with input autumn weight provided in parantheses on the abscissa. Predicted weights at starvation (reserve at 0 kg) are also given.

However, foraging energy measurements were originally taken on captive animals in pens  $2.4 \times 2.4$  m, with food at specific feeding platforms within the pens (Brocke 1970). The foraging energy expenditures measured therefore probably underestimate the energy expended by a wild opossum that will have to travel longer in cold ambient temperatures in search of food in unpredictable locations. Because increased foraging expenditure correlates to decreased survival probability, inaccuracy in the model representation of foraging energy is most likely to translate to over-optimistic survival expectations.

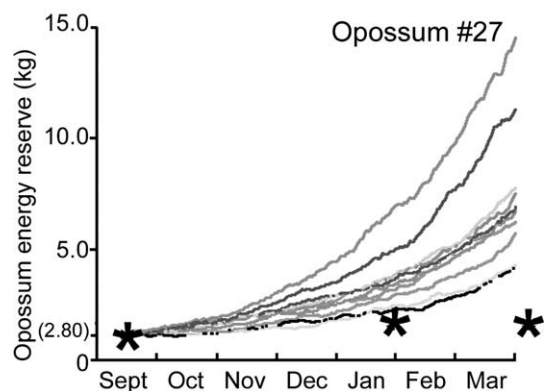
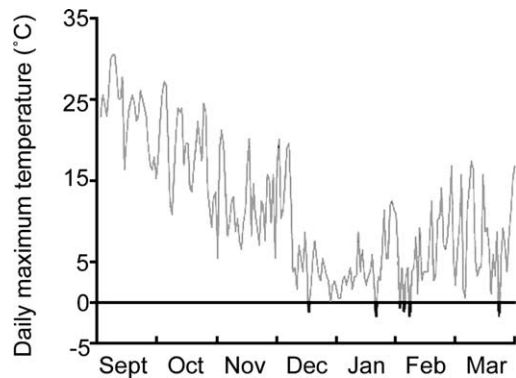
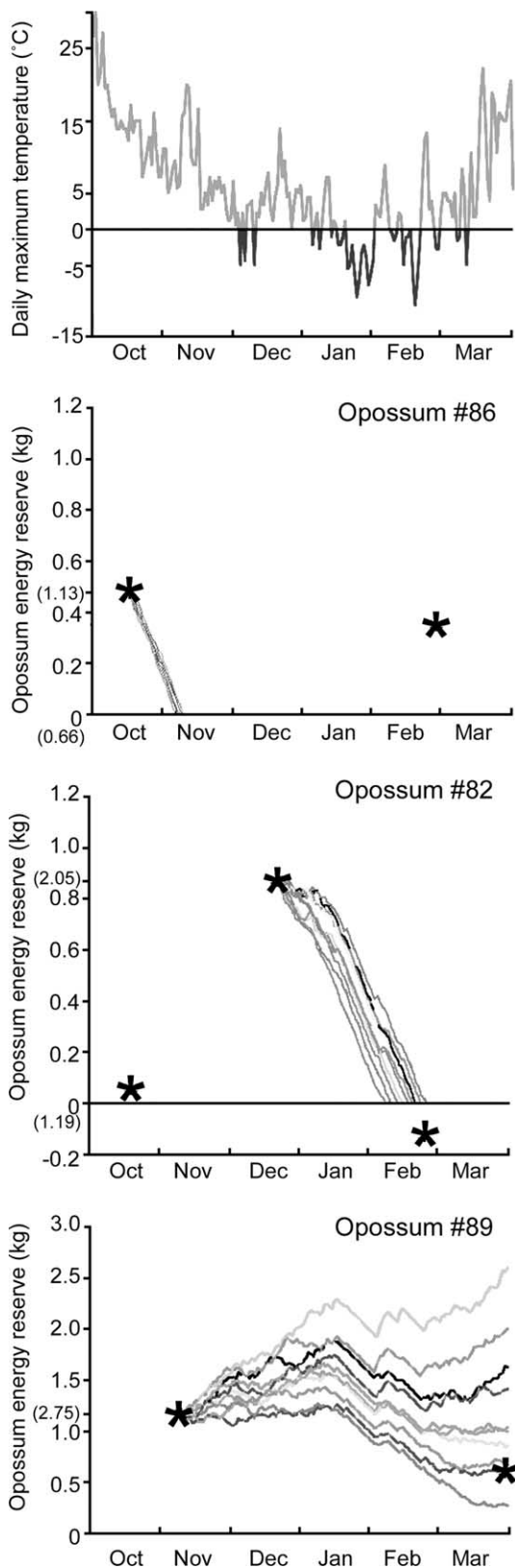


Fig. 7. Model output for simulation of animal #27 and the maximum daily temperatures recorded in the winter of 2001. For clarity, only 10 of the 1000 model runs for each animal is illustrated. \* denotes measured animal weights, with input autumn weight provided in parantheses on the abscissa.

The temperature at which the foraging decision is made can have a considerable effect upon opossum survival, depending upon how the change in decision temperature affects the number of foraging/non-foraging days. The total number of non-foraging days has a very large effect on opossum survival. A 2.59 kg opossum can have no more than 52 non-foraging days in order to survive over winter. With no more than 14 non-foraging days survival probability is expected to be 100%. When there are 14–52 non-foraging days, as is common in Amherst, MA, the order in which these non-foraging days occur may be very important, as documented by the wide variety in expected survival probabilities for the same number of non-foraging days calculated from different year-foraging decision combinations.

The most important influence on the model is not the potential variation in the energetic parameters of the model but the input of opossum weight. The size attained by the opossum by 1 December has a large effect on the probability of survival through the winter. Larger animals will have larger fat stores to draw upon and will be capable of taking and consuming larger prey (when available). Our sample included a number of such animals; however most of the larger animals were males.



The trouble for northern opossum populations is that the important class that must survive the winters are the juvenile females, which are the smallest individuals. The model predicted  $>67\%$  survival of average-sized (2.37 kg) females in only 4 of our 77 yr of time series, suggesting that populations should decline in most modeled years (Kanda and Fuller 2004). Of course, females in the real population have an unknown variance in size. However, if the female weights are normally distributed, and the mean females are not predicted to survive, then the 50% of the population that is smaller than average would also not be expected to survive. If stable demographics require  $\geq 67\%$  survival, then those years in which survival probability of the average female is low should also be characterized by low population persistence.

Replacement of lost animals via immigration is unlikely. While female opossums are known to disperse in the spring (with or without babies already in the pouch), most opossum dispersal distances are  $<7$  km (Gillette 1980), and the climate 10 km south of Amherst is not sufficiently different from Amherst to be hosting a source population. Further, immigration clearly cannot explain the recent occurrence of opossums 250 km north of Amherst (Gardner and Sunquist 2003).

The obvious discrepancy between these model predictions and the fact that opossum populations remain robust in and north of Amherst, MA, immediately calls into question the normally distributed foraging success model. However, comparison of the model with actual opossums followed in the Amherst area shows the strong predictive accuracy of the model. Given opossum weights close to the beginning of winter (November or December), the model correctly predicts the opossum's fate, including weight and date of death or the weight of surviving animals.

Exceptions were animal #80, who died earlier than anticipated by the model, and animal #63, who lived as expected but weighed less than predicted. Animal #80's death was probably accelerated by a large snowstorm on 26 December 2002 that apparently blocked the animal's den entrance. There was no evidence of foraging activity by #80 after the storm, and a mortality signal was received from the den three weeks later. Animal #63 spent at least four days not foraging before his death on 22 April from injuries, however at 23 g expended per resting day this accounts for only 92 g of the discrepancy between the actual weight (2.05 kg) and expected weight (2.65–4.65 kg).

Fig. 8. Model output for simulation of animals #86, #82, and #89, and the maximum daily temperatures recorded in the winter of 2002. For clarity, only 10 of the 1000 model runs for each animal is illustrated. \* denotes measured animal weights, with input autumn weights provided in parantheses on the abscissa. Predicted weights at starvation (reserve at 0 kg) are also given for animals predicted to die.

Table 4. Accuracy of normally distributed foraging success model variants in predicting (a) animal fates, and (b) live animal spring weights or starved animal death dates. ✓ indicates accurate prediction.

(a)														
	3 (die)	6 (die)	22 (live)	27 (live)	28 (live)	63 (live)	74 (live)	80 (die)	82 (die)	86 (die)	88 (die)	89 (live)	92 (live)	100 (live)
Null	✓	✓	✓	✓		✓	✓	✓	✓	✓	✓	✓	✓	✓
36% loss	✓	✓	✓	✓		✓	✓	✓	✓	✓	✓	✓	✓	✓
48% loss	✓	✓	✓	✓		✓	✓	✓	✓	✓	✓	✓	✓	✓
Resting 92 kcal	✓	✓	✓	✓		✓	✓	✓	✓	✓	✓	✓	✓	✓
Resting 112 kcal	✓	✓	✓	✓		✓	✓	✓	✓	✓	✓	✓	✓	✓
Foraging 123 kcal			✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓
Foraging 185 kcal	✓	✓		✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓
Decision -2°C		✓	✓	✓		✓	✓	✓	✓	✓	✓	✓	✓	✓
Decision 2°C	✓	✓	✓	✓		✓	✓	✓	✓	✓	✓	✓	✓	✓

(b)														
	Live weight							Death date						
	22	27	28	63	74	89	100	3	6	80	82	86	88	
Null	✓					✓	✓	✓	✓		✓		✓	
36% loss	✓					✓	✓	✓	✓		✓		✓	
48% loss	✓					✓	✓	✓	✓		✓		✓	
Resting 92 kcal	✓					✓	✓	✓	✓		✓		✓	
Resting 112 kcal	✓					✓	✓	✓	✓		✓		✓	
Foraging 123 kcal			✓			✓	✓	✓	✓		✓		✓	
Foraging 185 kcal				✓			✓	✓	✓	✓	✓		✓	
Decision -2°C	✓						✓	✓	✓	✓	✓		✓	
Decision 2°C	✓			✓				✓	✓	✓	✓		✓	

The model was less accurate when knowledge of the pre-winter opossum condition was obtained earlier in the autumn. In particular, juvenile animal #86 was predicted to die of starvation before winter even began. The model is designed to simulate winter foraging conditions, and does not consider the growth of young animals nor the foraging conditions available in the autumn. Because the total foraging energy gained in the model is dependant upon the size of the animal, the model limits energy intake of small animals during this pre-winter period. Instead of the autumn weight gain normally seen, the model predicts decreasing weight and starvation before winter despite foraging every night. Male #82 was weighed six days after #86, his sibling, and was 1.25 kg at the time (very similar to #86's 1.13 kg). However, by mid-December, #82 weighed 2.05 kg. I expect that #86 gained weight in a similar manner. This inability of the model to correctly simulate autumn conditions also accounts for the inaccurate predictions for the small adult #28.

The same principal model foraging success assumption may also account for the extraordinary and unrealistic weight gains predicted for two animals that lived comfortably through their respective winters (#27 and #74). Because these animals had higher pre-winter weights, the energy gained during each foraging bout was proportionally higher. Obviously there is a natural limit to the amount of energy gained in a bout (a limitation either of the animal's physical capacity or the

amount of food located), but the model does not impose such a limit. Thus as the model animal gained weight, the potential amount of food it gained also increased without limit, and large animals rapidly increased in weight.

Examination of predictions generated by variation of the parameters confirms that the null model was the most accurate. Reasonable variations in resting energy or percentage of weight loss do not alter the model. Changes in foraging energy expectations do have a major impact upon the model's predictive ability, as do changes in foraging decision temperature; interestingly, variations of these parameters tend to have lower predictive ability than the null model. I did not allow resting and foraging energy expenditures to vary with opossum weight, although Brocke (1970) indicated that heavier animals had higher expenditures; however, the model variants with higher expenditures did not have higher predictive power for the larger animals, and the model with higher foraging energy expenditures had decreased predictive power overall.

The reduced performance of the model with higher foraging energy expenditure is particularly curious, as I expect that wild opossum foraging expenditures tend to be higher than the average measured in captivity. Examination of models with differing foraging energy expenditure was equivalent to examination of models with constant foraging energy expenditure but differing foraging success, since the energy gained and energy

expended on a foraging day are subtracted from one another in the model. It is possible that the combination of 50% ad libitum foraging success and the mean measured foraging expenditure (i.e. the null model) resulted in a foraging-day energy gain similar to a higher foraging expenditure but also a higher mean intake in the actual animals.

The accuracy of the model in predicting actual opossum fates (when considering December through March) supports the validity of the general model predictions of poor survival for juveniles, and particularly for smaller female juveniles. If this model does in fact accurately represent the fates of opossums experiencing Amherst winters, then why do opossums exist in Amherst? The only two input variables are opossum autumn weight and winter temperatures. The winter temperatures reflected by the weather station may not represent the microclimates experienced by individual opossums throughout the local area. The other way in which the climate is represented in the model is through changes in the foraging decision temperature. While changing the foraging decision temperature rule did not increase predictive ability of the model for this sample of monitored animals, the influence of the decision rule varies greatly by year. In some years, the particular pattern of cold weather combined with a shift in the foraging decision temperature could greatly affect an opossum's survival probability.

The model suggests that the most important influence on opossum winter survival is the autumn weight of the individual. It is possible that our small sample of females does not accurately reflect the juvenile female population, and larger individuals such as #27 and #89 may better represent the population. If an animal has access to an abundant or high quality food source, it will enter winter in better condition and be better able to maintain itself over the course of the winter. Monitored females #27 and #89 suggest how this may occur: both animals lived in urban environments and used human-related resources, such as dining hall dumpsters, trash bins, and areas where humans deliberately left out food for wildlife.

The model supports the previous expectations that winter temperatures are a limiting factor on the northern range limit of the Virginia opossum. However, the opossum populations have expanded north beyond where regional winter temperatures alone would predict species limitation. Amherst, MA, serves as an example where winter temperatures should restrict opossum population persistence, yet the opossum population is well established in the urban areas. Despite it being one of the best-understood mammalian species distributional limits, closer examination suggests that mechanisms underlying the northern limit of Virginia opossums remain enigmatic. The model also suggests three major areas of inadequate understanding: the microclimates

actually experienced by opossums, the exact relationship of opossum foraging behavior with ambient temperature, and most importantly the role of additional factors, such as human-related resources, operating to mitigate the restrictive climatic effects. These factors can only be understood in greater detail through close monitoring of the behavior of individual opossums as they face northern winter conditions.

*Acknowledgements* – T. K. Fuller and P. R. Sievert supported both the fieldwork and manuscript. E. M. Jakob and J. Podos also provided valuable comments. J. T. Finn encouraged the model programming. The manuscript was greatly improved by suggestions from D. A. Kelt. The field work was supported by the USGS Massachusetts Cooperative Fish and Wildlife Research Unit, by a Grant-in-Aid of Research from Sigma Xi, the Scientific Research Society, by Max McGraw Wildlife Foundation, by a David J. Klingener Scholarship from the Massachusetts Museum of Natural History, and by the Cooperative State Research Extension, Education Service, U.S. Dept of Agriculture, Massachusetts Agricultural Experiment Station, under Project No. MAS0071. This is Massachusetts Agricultural Experiment Station Publication No. 3357.

## References

- Anon. 1997. Matlab student edition, ver. 5. – Mathworks, Natick, MA, USA.
- Anon. 1999. SAS, ver. 8. – SAS Inst., Cary, NC, USA.
- Blair, W. F. 1936. An opossum dies of cold and hunger. – *J. Mammal.* 17: 410.
- Brocke, R. H. 1970. The winter ecology and bioenergetics of the opossum, *Didelphis marsupialis*, as distributional factors in Michigan. – Ph.D. thesis, Michigan State Univ.
- de Vos, A. 1964. Range changes of mammals in the Great Lakes region. – *Am. Midl. Nat.* 71: 210–231.
- Gardner, A. L. 1982. Virginia opossum. – In: Chapman, J. A. and Feldhamer, G. A. (eds), *Wild mammals of North America: biology, management, and economics*. Johns Hopkins Univ. Press, pp. 3–36.
- Gardner, A. L. and Sunquist, M. E. 2003. Opossum. – In: Feldhamer, G. A., Thompson, B. C. and Chapman, J. A. (eds), *Wild mammals of North America: biology, management, and conservation*. Johns Hopkins Univ. Press, pp. 3–29.
- Gillette, L. N. 1980. Movement patterns of radio-tagged opossums in Wisconsin. – *Am. Midl. Nat.* 104: 1–12.
- Hossler, R. J., McAninch, J. B. and Harder, J. D. 1994. Maternal denning behavior and survival of juveniles in opossums in southeastern New York. – *J. Mammal.* 75: 60–70.
- Hsu, M., Harder, J. D. and Lustick, S. I. 1988. Seasonal energetics of opossums (*Didelphis virginiana*) in Ohio. – *Comp. Biochem. Physiol.* 90A: 441–443.
- Humphries, M. M., Thomas, D. W. and Speakman, J. R. 2002. Climate-mediated energetic constraints on the distribution of hibernating mammals. – *Nature* 418: 313–316.
- Kanda, L. L. 2005. Factors influencing survival and reproduction of Virginia opossums (*Didelphis virginiana*) at their northern distributional limit. – Ph.D. thesis, Univ. Massachusetts Amherst.
- Kanda, L. L. and Fuller, T. K. 2004. Demographic responses of Virginia opossums to limitation at their northern boundary. – *Can. J. Zool.* 82: 1126–1134.
- Long, C. A. and Copes, F. A. 1968. Note on the rate of dispersion of the opossum in Wisconsin. – *Am. Midl. Nat.* 80: 283–284.

- McNab, B. K. 2002. The physiological ecology of vertebrates. – Cornell Univ. Press.
- Peterson, R. L. and Downing, S. C. 1956. Distributional records of the opossum in Ontario. – *J. Mammal.* 37: 431–435.
- Pippitt, D. D. 1976. A radiotelemetric study of the winter energetics of the opossum *Didelphis virginiana* Kerr. – Ph.D. thesis, Univ. Kansas.
- Ryser, J. 1992. The mating system and male mating success of the Virginia opossum (*Didelphis virginiana*) in Florida. – *J. Zool.* 228: 127–139.
- Rosenzweig, M. L. 1995. Species diversity in space and time. – Cambridge Univ. Press.
- Seidensticker, J., O'Connell, M. A. and Johnsingh, A. J. T. 1987. Virginia opossum. – In: Novak, M. et al. (eds), Wild  
 furbearer management and conservation in North America. Ontario Trappers Assoc., pp. 247–261.
- Sunquist, M. E. and Eisenberg, J. F. 1993. Reproductive strategies of female *Didelphis*. – *Bull. Florida Mus. Nat. His.* 36: 109–140.
- Tyndale-Biscoe, H. 1973. Life of marsupials. – Edward Arnold.
- Wallace, A. R. 1876. The geographical distribution of animals. – Harper.
- Wiseman, G. L. and Hendrickson, G. O. 1950. Notes on the life history and ecology of the opossum in southeast Iowa. – *J. Mammal.* 31: 331–337.
- Wright, D. D. 1989. Mortality and dispersal of juvenile opossums, *Didelphis virginiana*. – M.S. thesis, Univ. Florida.

*Subject Editor: Douglas Kelt.*