

MODELING SURVIVAL RATES OF HIBERNATING MAMMALS WITH INDIVIDUAL-BASED MODELS OF ENERGY EXPENDITURE

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Estimating survival rates of naturally hibernating mammals is important for ecological and conservation reasons, but empirical estimates are logistically difficult to obtain. Individual-based models can estimate survival under circumstances that would be impossible or unethical to test experimentally. Here, we present an individual-based model based on energy expenditure to estimate survival rates of hibernating little brown bats (*Myotis lucifugus*). Initial simulations assumed only thermal energetics of individuals were important to energy expenditure; subsequent simulations assumed bats also use a behavioral mechanism (clustering) to reduce energy expenditure during euthermia. Our model suggests that survival rates are high (>0.96) for populations that cluster during hibernation and experience no human disturbance, regardless of winter length (between 90 and 200 d). Survival rates are much lower, especially at long winter lengths (0.73 ± 0.01 SD at 200 d), if bats do not cluster. Human disturbances strongly affect survival rates, but the relationship is not linear. Survival rates are not lowered substantially by a limited number of disturbances because those arousals would have occurred naturally, but as disturbances reach a frequency threshold (dependent on winter length and disturbance pattern) they become very detrimental to survival. Thus, our model has implications for understanding the effect of environmental variability, social thermoregulation, and human disturbance on mammals hibernating under natural conditions.

Key words: hibernation, individual-based model, *Myotis*, overwinter survival

Many physiological aspects of mammalian hibernation are well studied in the laboratory, but little is known about ecologically and demographically important variables such as survival rates during the season of hibernation. Empirical estimation of overwinter survival rates is hampered by several logistical limitations including the need for long-term data sets with intensive trapping effort in spring and autumn (e.g., in ground squirrels), sample-size limitations of radiotelemetric methods, or the inherent difficulty of capturing and recapturing individuals consistently enough for demographic analysis (e.g., in bats). Therefore, estimates of overwinter survival rates are available for only a limited number of species (e.g., Meaney et al. 2003; Schwartz et al. 1998; Sendor and Simon 2003), and generally are only available for a single population of a species under a specific set of environmental conditions.

The lack of knowledge about overwinter survival rates means it is difficult to establish whether factors affecting survival can be generalized across hibernators or if they are species specific.

For example, the length and severity of winter are obvious environmental factors that may affect survival during hibernation in some species, such as yellow-bellied marmots (*Marmota flaviventris*—Schwartz and Armitage 2005). However, other species, such as cave-dwelling bats, minimize the impact of winter severity by hibernating in protected caves and mines that moderate microclimate. Likewise, overwinter survival rates of some species may be affected by predation (Michener 2004), but predation may be rare for species or individuals hibernating in secure locations (Kokurewicz 2004).

Individual-based models offer a method to estimate population-wide demographic parameters by determining the fate of individuals (Goss-Custard et al. 2006a). Physiological and behavioral individual-based models have been successfully used to estimate survival in a variety of taxa (e.g., Goss-Custard et al. 2006b; Railsback et al. 2002) and provide at least 2 advantages when estimating survival rates. First, demographic estimates are an emergent property of the model instead of an input variable. Therefore, resulting survival estimates are not directly linked to the set of environmental conditions under which the original demographic data were collected (Goss-Custard et al. 2006a). Second, simulation models allow for modeling of survival under a range of conditions. Experimental estimates of survival rates under

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some conditions would be difficult or unethical to obtain because of logistical limitations in replication and the possibility that sampling-associated disturbances could cause population declines. For these reasons, individual-based models may be especially useful in estimating demographic parameters for species that are difficult to study under natural conditions, such as hibernating mammals.

Here we report the use of an individual-based model to estimate survival rates of a hibernating bat species and determine factors that may have the largest effect on survival rates. We include some factors that are specific to cavernicolous bats as examples of the specificity that can be achieved with these models, but we emphasize that similar models can be developed for any species difficult to study under natural conditions. We hope that this paper provides an example of the benefits of individual-based models in estimating survival rates in species where empirical estimates are logistically difficult to obtain.

MATERIALS AND METHODS

We chose to model survival rates for the little brown bat (*Myotis lucifugus*), a widespread, common, and well-studied species in North America. Some variables included have not been measured in little brown bats, so data from the ecologically similar Indiana bat (*Myotis sodalis*) are used when necessary. Calculations of energy expenditure by little brown bats during hibernation are well established (Humphries et al. 2005; Thomas et al. 1990) and this species has been successfully used in other bioenergetic models (Humphries et al. 2002).

Energetic expenditure.—We used a simple mathematical model to estimate energy expenditure during hibernation following a basic model previously used in several papers (Humphries et al. 2002, 2005; Thomas et al. 1990). In the simplest form, the entire energetic cost of winter (E_{win}) is calculated according to the equation:

$$E_{win} = E_{tor} + (n \times E_{bout}),$$

where E_{tor} is the energetic cost of torpor, n is the number of arousals, and E_{bout} is the energetic cost of a complete arousal:

$$E_{bout} = E_{ar} + E_{eu} + E_{cool},$$

where E_{ar} is the energetic cost of raising body temperature (T_b) to euthermic levels during arousals, E_{eu} is the cost of remaining euthermic, and E_{cool} is the cost while entering torpor (i.e., the lowering of T_b to heterothermic temperatures). We estimated E_{ar} and E_{eu} following Humphries et al. (2005):

$$E_{ar} = (T_{b-eu} - T_{b-tor})S$$

and

$$E_{eu} = BMR + (T_{lc} - T_a)C_{eu},$$

where T_{b-eu} is euthermic T_b , T_{b-tor} is torpid T_b , S is the specific heat capacity of body tissue, BMR is basal metabolic rate, T_{lc} is the lower critical limit of the thermal neutral zone, T_a is ambient temperature, and C_{eu} is euthermic thermal conductance. We used a constant value of 0.235 mW/g for torpid metabolic rate (TMR) at a minimum T_a of 5°C (Kelly 2003)

and estimated E_{cool} as 67% of the cost of E_{ar} (Thomas et al. 1990). Other values are from table 2.1 in Humphries et al. (2005). We assumed that 1 ml of oxygen releases 20.1 J and 1 mg of fat releases 39.3 J to convert energy calculations into fat expenditure (Nagy 1983).

Survival rates.—The purpose of this model is to estimate the effect of winter length, clustering, and human disturbances on survival rates of hibernating bats using individual-based estimates of energy expenditure. Each individual in the model enters winter with a unique body and fat mass and arouses with a unique pattern throughout winter. All individuals in a population are subjected to the same winter length, number and pattern of disturbances (see below), and each population either clusters in groups of greater than 5 individuals (Canals et al. 1997) or does not cluster.

We conducted simulations using the open-source programming language Python 2.5.1 (www.python.org). For each bat, we randomly chose a mass at the beginning of the hibernation season from the distribution $9.07 \text{ g} \pm 0.99 \text{ SD}$ (Johnson et al. 1998). We randomly selected the fat mass of each bat from a distribution with the mean value predicted by Kunz et al. (1998):

$$\text{fat mass} = -2.80 + (0.567 \times \text{mass}),$$

and the standard deviation calculated as:

$$\text{standard deviation of fat mass} = \frac{-1 + (0.2 \times \text{mass})}{3},$$

which approximates the variation around the regression line (Kunz et al. 1998). We randomly selected the length of each natural torpor bout from a distribution with a mean of 583.46 h and a standard deviation of 240 h, which approximate the measurements of Brack and Twente (1985) at 5°C. This created stochasticity in the arousal pattern of each bat throughout winter. All distributions were assumed to be normal.

We modeled winters in 1-h increments. During each hour of torpor, an individual expended energy at the rate estimated by TMR. At the end of each torpor bout, the individual expended energy equal to E_{bout} before resuming energy expenditure at TMR 3 h later (Thomas et al. 1990). We calculated survival rates for populations based on 12 winter lengths (90–200 d) that span the range of winter lengths experienced by hibernating bats in temperate regions. We defined winter as the period when bats cannot feed, and therefore cannot increase energy reserves, because prey is unavailable due to seasonally inclement weather.

We include human (i.e., unnatural) disturbances as a factor that may affect survival of cavernicolous bats during hibernation as an example of species-specific factors that can be incorporated into individual-based models. Arousal during hibernation is energetically expensive so arousal frequency is thought to decrease winter survival (Speakman et al. 1991; Thomas 1995). This idea has gained considerable reputation for hibernating bats because human disturbance increases arousal frequency. Although considered of great importance by ecologists and conservationists, the nature of the relationship between the level of disturbance and survival is not well quantified. Although it is

generally agreed that disturbances decrease survival rates, it is unknown whether the effects of disturbances are direct and proportional to the reduction in survival. Thus, managers often adopt a conservative approach to dealing with disturbances and prohibit all access during winter.

To estimate the effect of added, unnatural disturbances on survival, we created 1–25 disturbances distributed in 1 of 4 ways: uniformly, randomly, paired by 2, or daily. Uniform disturbances were distributed evenly across winter to simulate researchers making regular, scheduled visits to a hibernaculum. Random disturbances were distributed throughout winter to simulate disturbances at a hibernaculum with unrestricted public access. Paired distributions were simulated by randomly selecting hours during winter and adding a 2nd disturbance 24 h later. This simulates unprotected hibernacula visited mostly on weekends or holidays (although it does not necessitate periods of no disturbance during the week). Daily disturbances were simulated by randomly selecting 1 h during winter and then adding a disturbance every 24 h thereafter up to the total number of added disturbances (1–25). This simulates heavy, unregulated disturbances such as cave tours. We assume that each individual arouses at every disturbance. After each disturbance, the duration of the next torpor bout was selected for the natural arousal function and torpor bout length started over at 0.

One infrequently considered aspect of energy expenditure by hibernating bats is the benefit of clustering, which is likely important during euthermic periods (Boyles et al. 2008). Most cavernicolous species cluster to some extent, and even small clusters (5 individuals) significantly reduce heat loss by individuals (Canals et al. 1997; Kurta 1985). To estimate the energetic benefit of clustering, we ran all simulations with and without clustering. Based on theoretical estimates of Canals et al. (1997), we assumed that clustering lowered energy expenditure during euthermia to 41.1% of that expended when solitary. This assumes that most individuals in a cluster arouse synchronously, and are euthermic for the same period. In the case of unnatural disturbances, this is likely true, because most individuals of species that cluster arouse when researchers survey hibernacula containing large numbers of individuals (V. Brack, Jr., pers. obs.). Evidence of synchronous arousals during natural arousals is less clear, but we argue elsewhere that is likely (Boyles et al. 2008).

For each combination of winter length, number and pattern of disturbances, and clustering, we calculated survival in a population of 1,000 bats in 75 independent winters. An individual survived if its fat mass at the beginning of the season of hibernation was greater than the energy expended during the season. This may be conservative because mammals metabolize carbohydrates during the 1st few days of the season of hibernation and likely metabolize proteins throughout the season (Reidy and Weber 2004; Yacoe 1983). However, these are likely minor energy sources compared to stored body fat.

Sensitivity analysis.—We calculated the sensitivity of survival rates to variation in winter length, number of disturbances, pattern of disturbances, and clustering using a global analysis of variance–based sensitivity analysis (Ginot et al. 2006). Our resolution for the number of disturbances was

higher than necessary, so we pared our data set to include only winters with 2, 6, 10, 14, 18, or 22 disturbances. Our model suggests that without clustering, essentially no bats survive 14 disturbances regardless of other parameters. Even with clustering, survival at these disturbance rates is so low that, given the low reproductive rates of bats, populations likely could not persist. Further, the region above 14 disturbances had a large effect on the relative sensitivities of each parameter. Therefore, we also calculated sensitivity of survival rates for winters with 2–14 disturbances in intervals of 4. We report the sensitivity index of a factor as:

$$S_{\text{effect}} = \frac{SS_{\text{effect}}}{SS_{\text{total}}},$$

where SS_{effect} is the sum of squares of the effect and SS_{total} is the total sum of squares. We also report the total sensitivity index of each main factor, which is the sum of sensitivity indices for all effects in which a factor is involved (Ginot et al. 2006).

Limitations of the model.—We estimate energy expenditure of all individuals using a single, minimum TMR value. This is most realistic if all individuals hibernate at the T_a that maximizes energy conservation; however, individuals with large energy reserves may choose to hibernate at warmer temperatures (Boyles et al. 2007a; Kokurewicz 2004). This may slightly decrease survival rates estimated by our model because individuals that hibernate at warm temperatures will expend energy faster than minimum TMR. However, hibernacula that support large numbers of bats are often large and have wide thermal gradients, so individuals have colder temperatures available to them if they become energetically stressed. Our model may need to be altered for caves where the T_a that maximizes energy conservation is not available. Further, the validity of TMR measurements also may affect the model, but the model was relatively insensitive to large changes in TMR values. Also, there is likely individual and regional variation in metabolic rates and body composition that are unknown that we did not consider. This may be important because we consider winter lengths representative of large parts of the temperate regions. Additionally, not all bats follow the same phenological pattern (Twente 1955) and there are insufficient data to accurately estimate the hibernation season of individual bats. We consider winter length static for a population, but variation in the length of season during which an individual hibernates may profoundly affect survival. Finally, clustering while euthermic is the only method of behavioral thermoregulation we consider, although there may be others. Clustering also may lessen the cost of raising T_b to euthermic levels and bats often move to the warmest part of the cave when euthermic, which may reduce heat loss to the environment.

RESULTS

Effects of winter length, clustering, and disturbances on survival rates.—All derivations of our model produce survival curves with similar shapes, but clustering substantially changes the slope of the curve (Fig. 1). When bats do not cluster,

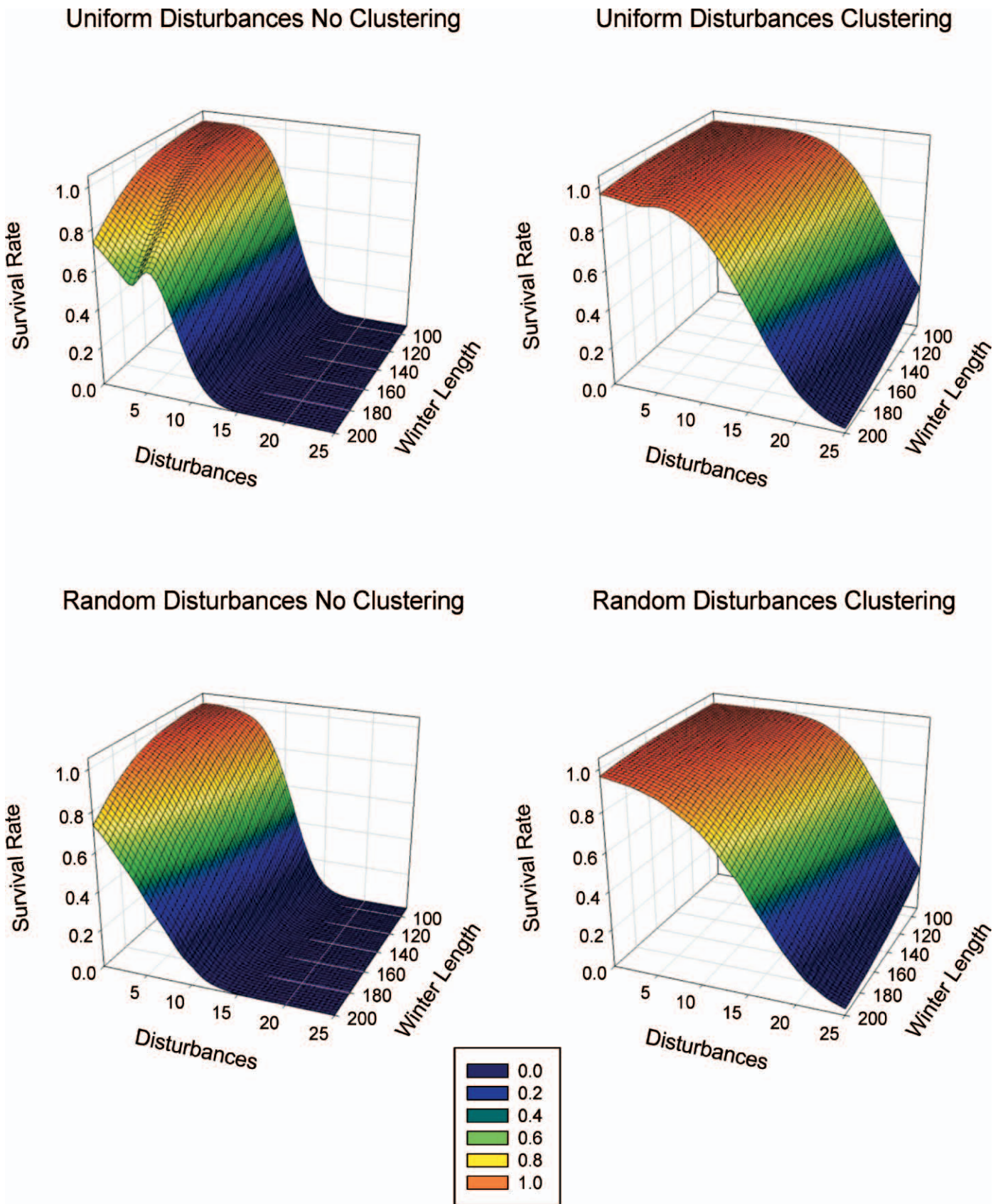
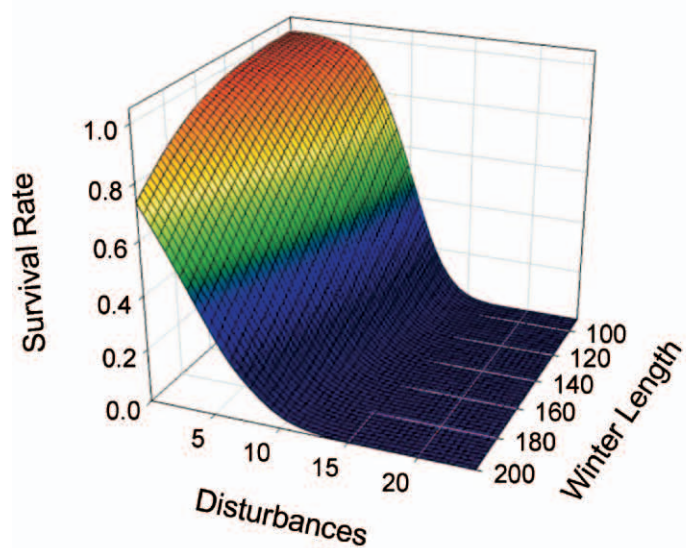
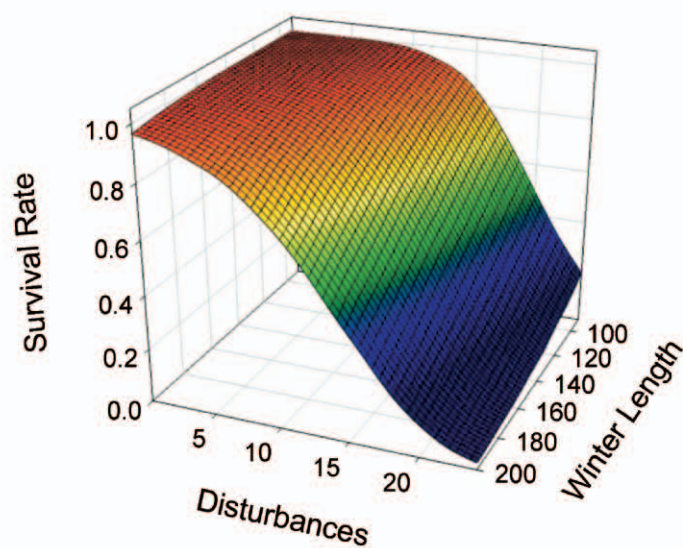


FIG. 1.—Survival estimate curves generated by computer simulations. These graphs show the curves obtained when unnatural disturbances are uniformly distributed throughout winter and when bats cluster and do not cluster during euthermic periods. Colors represent the gradient of survival rates.

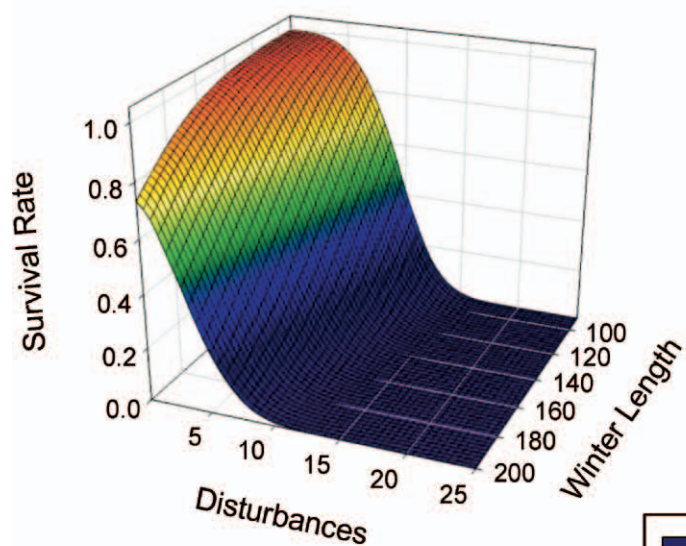
Disturbances Paired by Two No Clustering



Disturbances Paired by Two Clustering



Daily Disturbances No Clustering



Daily Disturbances Clustering

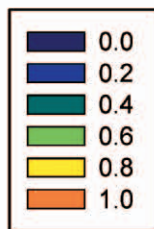
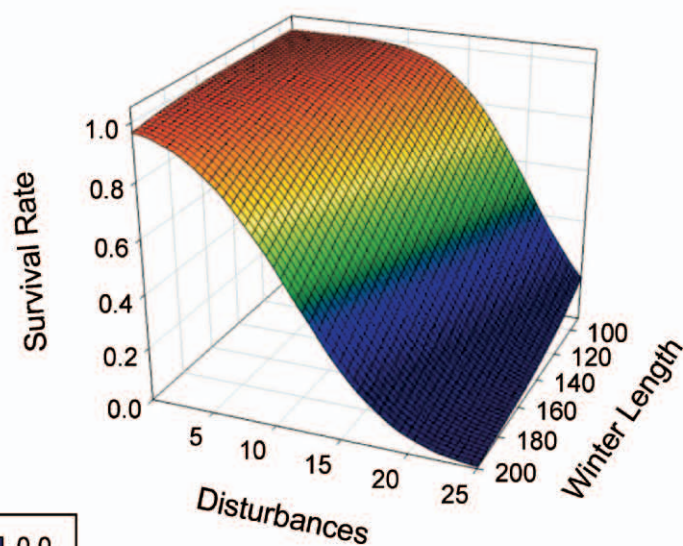


FIG. 1.—Continued.

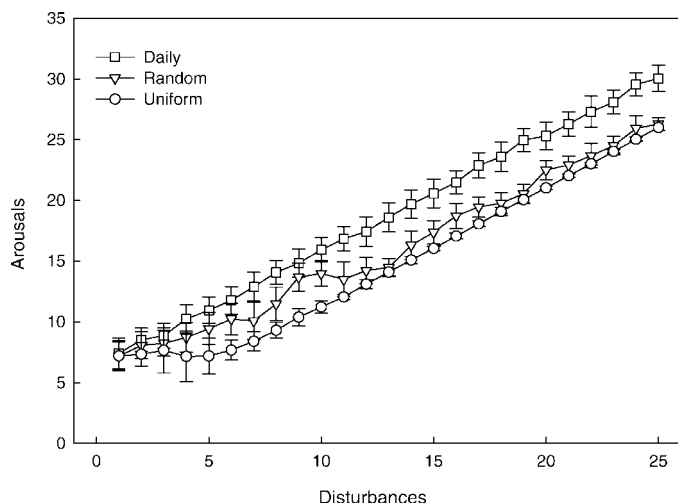


FIG. 2.—Relationship between number of disturbances and number of arousals for a 150-d winter under uniform, random, or daily disturbance patterns (disturbances in groups of 2 are excluded for clarity). Values are mean $\pm$ *SD* obtained from simulations of 100 individuals. These simulations were done separately from those reported in the results.

survival rates are high for short winters with few disturbances. As winter length or number of disturbances increases, survival rates drop. For example, with no disturbances, survival drops from 0.998 ± 0.002 *SD* during a 90-d winter to 0.734 ± 0.013 during a 200-d winter. The survival rate in a 150-d winter with no disturbances is 0.953 ± 0.007 but drops to 0.692 ± 0.015 with 8 uniformly distributed disturbances.

Clustering increased the combinations of winter lengths and disturbances at which survival is sufficient for the population to persist. Even at the longest winter modeled, 200 d, estimated survival of clustered bats is 0.963 ± 0.006 . Likewise, disturbances are less detrimental when bats cluster. In a 150-d winter, the survival rate is 0.995 ± 0.002 for populations that experience no disturbances and 0.979 ± 0.003 in populations disturbed uniformly 8 times.

The pattern of disturbance has subtle effects on survival rates, with disturbances becoming more detrimental (i.e., the slope of the survival curve becomes more negative) when disturbances are more clumped. For example, survival rates of clustered populations disturbed 8 times during a 150-d winter are 0.979 ± 0.003 , 0.959 ± 0.008 , 0.939 ± 0.011 , and 0.912 ± 0.009 for uniform, random, paired, and daily disturbance patterns, respectively.

The relationship between the number of disturbances and survival is likely explained by the increase in the average number of arousals as the number of disturbances increase. This relationship varies with the disturbance pattern when there are few disturbances, but all become essentially linear as the number of disturbances increases (Fig. 2). It is important to note that at low disturbance frequencies, each disturbance does not add 1 average arousal to the population, especially when disturbances are randomly or uniformly spaced.

Sensitivity analyses.—In both sensitivity analyses (winters with 2–22 disturbances and 2–14 disturbances), a model with

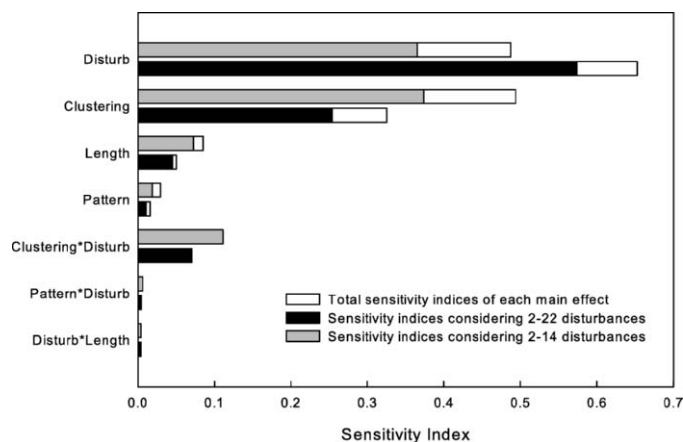


FIG. 3.—Results of global analysis of variance-based sensitivity analyses showing the individual and total sensitivities of each factor modeled when winters with 2–22 disturbances and winters with 2–14 disturbances are included in the analysis. “Disturb” is the number of unnatural disturbances during the winter; “Clustering” indicates whether clustering during euthermia was included in the analysis; “Length” is the number of days during a simulated winter; and “Pattern” is the temporal spacing of unnatural disturbance: uniform, random, paired, or daily.

only main effects and 2nd-order interactions explained most of the variance (96.4% and 96.3%, respectively); therefore, we did not include higher-level interactions. The output of both analyses generally met assumptions of null residuals, but neither perfectly fulfilled the assumption of homogeneity of variance (Ginot et al. 2006). No simple transformations improved the homoscedasticity of the data, so analyses were conducted on raw data.

In both analyses, survival is very sensitive to the number of disturbances and clustering. For winters with 2–22 disturbances, the number of disturbances has a total sensitivity index of 0.653 and clustering has a total sensitivity index of 0.325 (Fig. 3). When considering only winters with 2–14 disturbances (which removes biologically unimportant disturbances after nonclustering bats have died), relative sensitivities change considerably. In this scenario, clustering has a total sensitivity index of 0.494 and the number of disturbances has a total sensitivity index of 0.487. In both analyses, the next most important factor is the interaction between clustering and number of disturbances, with sensitivity indexes of 0.071 and 0.111 for 2–22 and 2–14 disturbances, respectively. The length of winter and pattern of disturbances are less important to estimated survival rates in both analyses (total sensitivities < 0.085).

DISCUSSION

High survival rates are typical of species with a long life span and low reproductive output, typical of most bats. However, virtually no estimates of overwinter survival are available for hibernating bat species because of the inherent difficulties involved with studying these species (but see Sendor and Simon 2003). Our model estimates that winter survival of little brown bats is generally above 0.96 in

undisturbed populations that cluster during euthermic periods. These estimates are considerably higher than many reported annual survival rates for bats (Hoyle et al. 2001; Pryde et al. 2005), including North American myotis bats (Boyles et al. 2007b; Frick et al. 2007; Keen and Hitchcock 1980). If we assume that these estimates are accurate and mortality is low during hibernation for reasons we did not model (e.g., predation, freezing, or dehydration), then either high emigration causes artificially low estimates of annual survival or most mortality occurs outside the season of hibernation. For example, mortality during migration between hibernacula and summer roosting areas (Tuttle and Stevenson 1977) and predation during the breeding season (Pryde et al. 2005) lower annual survival rates.

Behavioral thermoregulation via clustering appears important for survival during hibernation. When considering only winters with <14 disturbances, clustering has a larger effect on survival rates than any other factor. This suggests that purely physiological models (the equivalent of no clustering in this model) may underestimate survival rates of hibernating bats because they do not consider benefits of behavioral thermoregulation for energy conservation. Not all bat species cluster during hibernation, but those that do not tend to hibernate at warmer temperatures (McNab 1974) where heat loss to the environment during euthermic periods is lessened.

The other main factor affecting survival of hibernating little brown bats is the number of disturbances. It is important that the relationship between disturbances and survival is not linear. When clustering is considered, the 1st several disturbances cause no appreciable drop in survival, but each disturbance above some frequency threshold causes a large drop in the survival rate. When disturbances are uniform during winters longer than 120 d, the threshold where disturbances become highly detrimental is approximately equal to the average number of natural arousals in undisturbed hibernacula. During winters shorter than 120 d, the threshold is higher. If disturbances are random, paired, or daily, the threshold is lowered. Further, our model simulates only the effects of nontactile disturbances on survival rates. Tactile disturbances may cause bats to expend more energy (Speakman et al. 1991) and may change the point at which disturbances substantially lower survival.

Our sensitivity analyses indicate that winter length has a smaller effect on survival rates than clustering or disturbance. Therefore, it may benefit bats that hibernate in secure, undisturbed hibernacula to winter farther north. This would expose bats to longer winters and a slightly lower probability of winter survival, but it may increase overall survival by allowing them to avoid energetic costs and mortality associated with migration (Tuttle and Stevenson 1977). The changing distribution of overwintering populations of endangered Indiana bats (*M. sodalis*) may provide an interesting, albeit anecdotal case study. The winter distribution of this species has shifted north as hibernacula throughout the range are protected and abandoned mines become available as hibernacula. This northerly shift may be a response to climate change (sensu Humphries et al. 2002, 2004); however, an alternate explanation

is that protection of hibernacula essentially removes the effect of disturbances on survival rates and makes winter length the only consideration. Because the effect of winter length on survival rates is small, Indiana bats may choose to remain farther north, nearer summer habitat, instead of migrating to areas with shorter winters. In general, cave populations in northern parts of the range have increased after protection of the cave, whereas populations in southern caves have decreased after protection (Currie 2002). Before protection of hibernacula, survival costs imposed by disturbances during long winters may have outweighed survival costs of migration to more southerly locations.

We used an individual-based model to estimate survival rates of a species for which overwinter survival rates cannot yet be measured empirically. Generally, our goal was to use an individual-based model to address ecological and conservation questions related to hibernating mammals. Specifically, we used this model to predict the effects of clustering, winter length, and human disturbances on survival rates of hibernating little brown bats. Verification of the model is important, but it is unlikely this can be done by directly measuring survival. More realistically, we suggest that verification involve using the model to predict body mass of known individuals and then weighing those individuals before and after the hibernation season. If the model accurately predicts weight loss, we argue that it can likely be assumed to accurately estimate survival.

After testing, our model may be an important tool when making conservation decisions relating to bats such as predicting the suitability of mines as potential hibernacula, thereby improving efficiency of acquiring and protecting hibernacula. Similar models can be used to address a variety of questions regarding the ecology and conservation of hibernating bats as well as other hibernating mammals. For example, bioenergetic models (Humphries et al. 2002, 2004) could be incorporated into individual-based models to predict effects of climate change on population or species-wide demographic variables. As similar models of additional species are parameterized and tested, generalizations about important factors affecting demographic parameters of hibernating species will become more robust. Further, as models are refined, additional testable predictions of basic ecology as well as the efficacy of conservation and management efforts will undoubtedly emerge.

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LITERATURE CITED

- BOYLES, J. G., M. B. DUNBAR, J. J. STORM, AND V. BRACK, JR. 2007a. Energy availability influences microclimate selection of hibernating bats. *Journal of Experimental Biology* 210:4345–4350.
- BOYLES, J. G., J. J. STORM, AND V. BRACK, JR. 2008. Thermal benefits of clustering during hibernation: a field test of competing hypotheses on *Myotis sodalis*. *Functional Ecology* 22:632–636.

- BOYLES, J. G., B. L. WALTERS, J. O. WHITAKER, JR., AND J. B. COPE. 2007b. A reanalysis of apparent survival rates of Indiana myotis (*Myotis sodalis*). *Acta Chiropterologica* 9:127–132.
- BRACK, V., JR., AND J. W. TWENTE. 1985. The duration of the period of hibernation of three species of vespertilionid bats. I. Field studies. *Canadian Journal of Zoology* 63:2952–2954.
- CANALS, M., M. ROSENMAN, AND F. BOZINOVIC. 1997. Geometrical aspects of the energetic effectiveness of huddling in small mammals. *Acta Theriologica* 42:321–328.
- CURRIE, R. R. 2002. Response to gates at hibernacula. Pp. 86–98 in *The Indiana bat: biology and management of an endangered species* (A. Kurta and J. Kennedy, eds.). Bat Conservation International, Austin, Texas.
- FRICK, W. F., W. E. RAINEY, AND E. D. PIERSON. 2007. Potential effects of environmental contamination on Yuma myotis demography and population growth. *Ecological Applications* 17:1213–1222.
- GINOT, V., S. GABA, R. BEAUDOUIN, F. ARIES, AND H. MONOD. 2006. Combined use of local and ANOVA-based global sensitivity analyses for the investigation of a stochastic dynamic model: application to the case study of an individual-based model of a fish population. *Ecological Modelling* 193:479–491.
- GOSS-CUSTARD, J. D., ET AL. 2006a. Test of a behavior-based individual-based model: Response of shorebird mortality to habitat loss. *Ecological Applications* 16:2215–2222.
- GOSS-CUSTARD, J. D., P. TRIPLET, F. SUEUR, AND A. D. WEST. 2006b. Critical thresholds of disturbance by people and raptors in foraging wading birds. *Biological Conservation* 127:88–97.
- HOYLE, S. D., A. R. POPE, AND G. J. TOOP. 2001. Mark–recapture may reveal more about ecology than about population trends: demography of a threatened ghost bat (*Macroderma gigas*) population. *Austral Ecology* 26:80–92.
- HUMPHRIES, M. M., J. R. SPEAKMAN, AND D. W. THOMAS. 2005. Temperature, hibernation energetics, and the cave and continental distributions of little brown myotis. Pp. 23–37 in *Functional and evolutionary ecology of bats* (A. Zubaid, G. F. McCracken, and T. Kunz, eds.). Oxford Press, Oxford, United Kingdom.
- HUMPHRIES, M. M., D. W. THOMAS, AND J. R. SPEAKMAN. 2002. Climate-mediated energetic constraints on the distribution of hibernating mammals. *Nature* 418:313–316.
- HUMPHRIES, M. M., J. UMBANHOWAR, AND K. S. MCCANN. 2004. Bioenergetic prediction of climate change impacts on northern mammals. *Integrative and Comparative Biology* 44:152–162.
- JOHNSON, S. A., V. BRACK, JR., AND R. E. ROLLEY. 1998. Overwinter weight loss of Indiana bats (*Myotis sodalis*) from hibernacula subject to human visitation. *American Midland Naturalist* 139:255–261.
- KEEN, R., AND H. B. HITCHCOCK. 1980. Survival and longevity of the little brown bat (*Myotis lucifugus*) in southeastern Ontario. *Journal of Mammalogy* 61:1–7.
- KELLY, S. A. 2003. Ambient temperature effects on metabolism and body composition in torpid bats (*Myotis lucifugus* and *Pipistrellus subflavus*). M.S. thesis, Missouri State University, Springfield.
- KOKUREWICZ, T. 2004. Sex and age related habitat selection and mass dynamics of Daubenton's bats *Myotis daubentonii* (Kuhl, 1817) hibernating in natural conditions. *Acta Chiropterologica* 6:121–144.
- KUNZ, T. H., J. A. WRAZEN, AND C. D. BURNETT. 1998. Changes in body mass and fat reserves in prehibernating little brown bats (*Myotis lucifugus*). *Ecoscience* 5:8–17.
- KURTA, A. 1985. External insulation available to a non-nesting mammal, the little brown bat (*Myotis lucifugus*). *Comparative Biochemistry and Physiology, A. Comparative Physiology* 82: 413–420.
- MENAB, B. K. 1974. The behavior of temperate cave bats in a subtropical environment. *Ecology* 55:943–958.
- MEANEY, C. A., A. K. RUGGLES, B. C. LUBOW, AND N. W. CLIPPINGER. 2003. Abundance, survival, and hibernation of Preble's meadow jumping mice (*Zapus hudsonicus preblei*) in Boulder County, Colorado. *Southwestern Naturalist* 48:610–623.
- MICHENER, G. R. 2004. Hunting techniques and tool use by North American badgers preying on Richardson's ground squirrels. *Journal of Mammalogy* 85:1019–1027.
- NAGY, K. A. 1983. The doubly-labelled water ($^3\text{H}^18\text{O}$) method: a guide to its use. University of California, Los Angeles Publication 12–1417:1–45.
- PRYDE, M. A., C. F. J. O'DONNELL, AND R. J. BARKER. 2005. Factors influencing survival and long-term population viability of New Zealand long-tailed bats (*Chalinolobus tuberculatus*): implications for conservation. *Biological Conservation* 126:175–185.
- RAILSBACK, S. F., B. C. HARVEY, R. H. LAMBERSON, D. E. LEE, N. J. CLAASEN, AND S. YOSHIHARA. 2002. Population-level analysis and validation of an individual-based cutthroat trout model. *Natural Resource Modeling* 15:83–110.
- REIDY, S. P., AND J.-M. WEBER. 2004. Metabolism of normothermic woodchucks during prolonged fasting. *Journal of Experimental Biology* 207:4525–4533.
- SCHWARTZ, O. A., AND K. B. ARMITAGE. 2005. Weather influences on demography of the yellow-bellied marmot (*Marmota flaviventris*). *Journal of Zoology (London)* 265:73–79.
- SCHWARTZ, O. A., K. B. ARMITAGE, AND D. VAN VUREN. 1998. A 32-year demography of yellow-bellied marmots (*Marmota flaviventris*). *Journal of Zoology (London)* 246:337–346.
- SENDOR, T., AND M. SIMON. 2003. Population dynamics of the pipistrelle bat: effects of sex, age and winter weather on seasonal survival. *Journal of Animal Ecology* 72:308–320.
- SPEAKMAN, J. R., P. I. WEBB, AND P. A. RACEY. 1991. Effects of disturbance on the energy expenditure of hibernating bats. *Journal of Applied Ecology* 28:1087–1104.
- THOMAS, D. W. 1995. Hibernating bats are sensitive to nontactile human disturbance. *Journal of Mammalogy* 76:940–946.
- THOMAS, D. W., M. DORAIS, AND J. M. BERGERON. 1990. Winter energy budgets and cost of arousals for hibernating little brown bats, *Myotis lucifugus*. *Journal of Mammalogy* 71:475–479.
- TUTTLE, M. D., AND D. E. STEVENSON. 1977. An analysis of migration as a mortality factor in the gray bat based on public recoveries of banded bats. *American Midland Naturalist* 97:235–240.
- TWENTE, J. W., JR. 1955. Some aspects of habitat selection and other behavior of cavern-dwelling bats. *Ecology* 36:706–732.
- YACOE, M. E. 1983. Protein metabolism in the pectoralis muscle and liver of hibernating bats, *Eptesicus fuscus*. *Journal of Comparative Physiology, B. Biochemical, Systemic, and Environmental Physiology* 152:137–144.

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