

TRAP-INDUCED MASS DECLINES IN SMALL MAMMALS: MASS AS A POPULATION INDEX

DEAN E. PEARSON,¹ U.S. Forest Service, Rocky Mountain Research Station, Forestry Sciences Laboratory, Box 8089, Missoula, MT 59807, USA

YVETTE K. ORTEGA, U.S. Forest Service, Rocky Mountain Research Station, Forestry Sciences Laboratory, Box 8089, Missoula, MT 59807, USA

LEONARD F. RUGGIERO, U.S. Forest Service, Rocky Mountain Research Station, Forestry Sciences Laboratory, Box 8089, Missoula, MT 59807, USA

Abstract: Body mass is routinely used as an index of physical condition for comparing small-mammal populations. However, trapping effects on animals may undermine the effectiveness of body mass as an index of population health. We examined the effects of live-trapping on body mass of 3 small-mammal species: deer mice (*Peromyscus maniculatus*), southern red-backed voles (*Clethrionomys gapperi*), and red-tailed chipmunks (*Tamias ruficaudus*). We found that live-trapping resulted in significant trap-induced body mass declines (TMDs) that varied by species, age, and sex. Longer rest intervals between captures reduced TMDs in deer mice, but not in other species. The TMDs were more dramatic for deer mice that died in traps than for those that did not, suggesting that TMDs may induce trap mortality and reduce survivorship in small mammals that are live-trapped. The proximate causes of TMDs remain unknown, but dehydration and hypothermia are likely causal agents. Since TMDs vary by species, age, and sex, and exposure to heating and cooling vary in space and time (e.g., by habitat and season), body mass as measured by live-trapping appears to be a negatively biased index whose deviation from true mass may vary among study populations and demographic groups. Researchers can attempt to bias correct indices of body mass using regression approaches, but such adjustments require large samples to be robust and so may not necessarily improve the raw indices. Additional research is needed to identify the causes of TMDs to better understand biases associated with using body mass as a population index and minimize impacts on small mammals.

JOURNAL OF WILDLIFE MANAGEMENT 67(4):684–691

Key words: body mass, *Clethrionomys gapperi*, deer mice, indices, live-trapping, Montana, *Peromyscus maniculatus*, red-backed voles, red-tailed chipmunks, small mammals, survivorship, *Tamias ruficaudus*, trap mortality.

Sampling effects are virtually inescapable consequences of ecological research. Good study designs attempt to minimize these effects to the point that researchers can safely assume that sampling methods do not confound the results of an otherwise “controlled” experiment. However, testing for sampling effects is less common than it should be, given the influence such effects can have on research results.

Body mass is recognized as an index of physical condition for vertebrates and is routinely used as an indicator of habitat quality in studies of small-mammal populations (e.g., Albers et al. 1990, Peles and Barrett 1996, Nupp and Swihart 1998, Von Trebra et al. 1998). Although this is a reasonable assumption, the effect of live-trapping may undermine the efficacy of body mass as an index of population health. Numerous studies suggest that live-trapping reduces small mammal body mass (Korn 1987, Slade and Iskjaer 1990, Slade 1991, Schon and Korn 1992). Therefore, measures of body mass from animals captured in

live-traps appear to generate a negatively biased index of true body mass. Although less accurate than an unbiased estimate, a negatively biased index is not problematic for comparative studies so long as the bias is constant (see discussions in McKelvey and Pearson 2001). However, because little is known about the causes of TMDs, the consistency of the bias is also in question.

Researchers have linked trap mortality with exposure of individuals to heat and cold (Perrin 1975, Gurnell 1982, Schon and Korn 1992, Kaufman and Kaufman 1994), conditions that vary over space and time. Furthermore, sensitivity to trap conditions appears to differ by age and sex (Slade 1991, Kaufman and Kaufman 1994). Effects of trapping on body mass may also vary as a function of habitat, season, and demographic composition of the population. Yet researchers have frequently used body mass measurements averaged across age or sex groups to compare physical condition of populations in disparate habitats or seasons (e.g., Albers et al. 1990, Sullivan et al. 1998, Von Trebra et al. 1998). If TMDs are not constant among study populations, then measured differences in body mass among populations may reflect

¹ E-mail: dpearson@fs.fed.us

differential trap effects rather than actual differences in physical condition or habitat quality.

Mass declines caused by live-trapping may also impact populations under study. Body mass of small mammals has been correlated with important demographic traits such as fecundity and survival (McClenaghan and Gaines 1978, Myers and Master 1983, Sauer and Slade 1986). Therefore, trapping could have significant effects on survival and fitness that vary among study populations, introducing further bias into study results. If mass declines are cumulative, repeated captures of individuals may be degenerative and ultimately cause mortality, either in the trap or after release. Although some researchers have offered evidence of cumulative effects of mass declines (Bietz et al. 1977, Korn 1987, Slade 1991), others suggest that mass declines are not cumulative (Perrin 1975, Kaufman and Kaufman 1994). In addition, rest intervals between captures may reduce the severity of TMDs, but this question has not been examined.

We used field data to examine effects of live-trapping on body mass of 3 species of small mammals. To assess the nature of trapping effects on demographic groups, we compared mass change among age and sex classes. We also evaluated the relationship between mass change and trap mortality and considered the influence of rest intervals. We discuss the implications of using a negatively biased index of body mass in studies of small-mammal populations and propose a method for bias correction.

METHODS

We conducted live-trapping from May through July of 1996 and 1997 at 10 coniferous forest sites in west-central Montana, USA. Sites were dominated primarily by ponderosa pine (*Pinus ponderosa*), western larch (*Larix occidentalis*), and Douglas-fir (*Pseudotsuga menziesii*). Three transects and 3 grids of 25 Sherman live-traps (H. B. Sherman Traps, Tallahassee, Florida, USA) spaced at 10-m intervals were placed at each of the 10 sites. We placed an additional transect and grid at 1 site in both years (i.e., 4 transects and 4 grids total), and a second site had twice as many traps in 1996 (49 traps on each grid and transect) as in 1997. A third site had 2 additional transects, and a fourth site had 1 additional grid in both years. We set traps for 8 consecutive days for a total of 27,152 trap nights for the 2 years. Traps were baited with approximately 2 to 3 tablespoons of peanut butter and whole oats and checked each morning. We

did not use bedding material in traps because handling bedding material despoiled with rodent excreta could increase the risk of *Hantavirus* infection in the field (e.g., Mills et al. 1995), and because effectiveness of bedding material for alleviating trap stress has not been substantiated.

Upon initial capture, we identified each individual to species, determined sex and reproductive condition, applied a No. 1005-1 monel ear tag (National Band and Tag Company, Newport, Kentucky, USA), and determined body mass using Pesola spring-balanced scales (Pesola, Baar, Switzerland). Animals were reexamined and reweighed at each subsequent capture. Deer mice and southern red-backed voles were weighed to the nearest 0.5 g using 60-g scales (0.5-g increments, accuracy $\pm 0.3\%$), and red-tailed chipmunks were weighed to the nearest 1 g using 100-g scales (1.0-g increments, accuracy $\pm 0.3\%$). We weighed deer mice and southern red-backed voles by the tail to avoid errors associated with tare weights. We weighed red-tailed chipmunks in bags and tared their final weights. We assigned animals to either adult or juvenile age-classes based on examination of mass distributions from initial body mass: juveniles were ≤ 16.5 g for deer mice, ≤ 17.5 g for red-backed voles, and ≤ 40 g for red-tailed chipmunks. We considered females pregnant if the lower abdomen was visibly or palpably swollen, if parturition occurred in traps, or if they showed evidence of parturition between captures (i.e., an acute drop in mass in 24 hr).

We evaluated the effect of trapping on body mass by examining masses measured over successive captures using a mixed linear model (Proc Mixed; SAS Institute 1999). Masses obtained for each individual over a series of at least 2 captures were treated as repeated measures using an autoregressive time series framework. For overall tests of mass change by species, we evaluated capture number as a covariate; and incorporated sex, age, and their interaction as fixed effects. We then added the interactions of capture number with both age and sex to the basic model to evaluate whether the process of mass change differed by age or sex. To consider the influence of rest intervals on recapture masses, we incorporated days since last capture (i.e., time between recaptures) into the basic model as a covariate and evaluated its interaction with capture number. We also included interactions among days since last capture, capture number, and age and sex, respectively. Finally, to examine the relationship between trapping effects and mortality, we used the basic

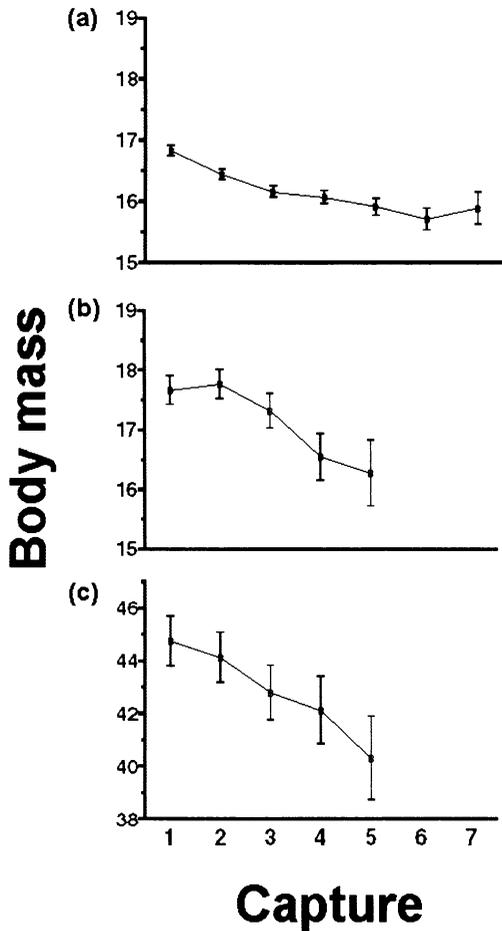


Fig. 1. Changes in body mass (g) with repeated captures presented as adjusted means (\pm SE) for (a) deer mice, (b) red-backed voles, and (c) red-tailed chipmunks live-trapped in Montana, USA, 1996 and 1997.

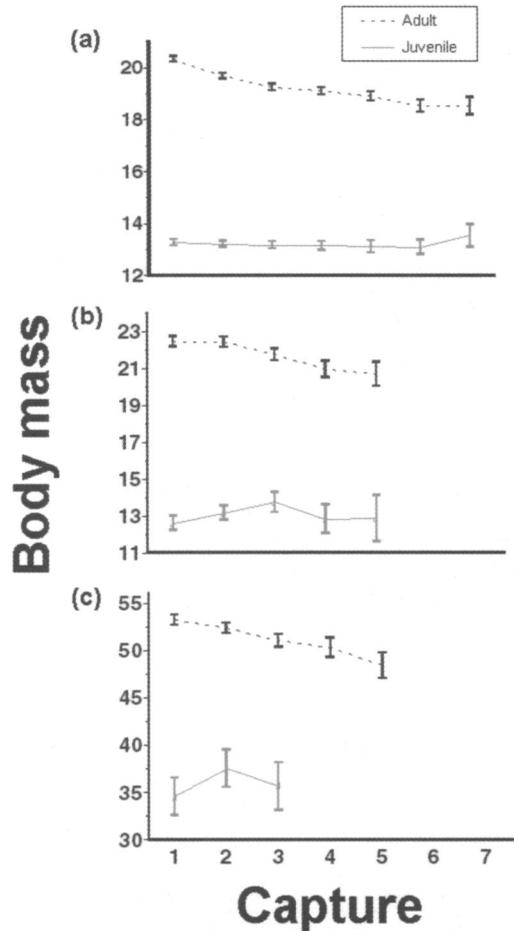


Fig. 2. Changes in body mass (g) with repeated captures presented as adjusted means (\pm SE) for adult versus juvenile (a) deer mice, (b) red-backed voles, and (c) red-tailed chipmunks live-trapped in Montana, USA, 1996 and 1997.

model to compare mass changes of animals that died in traps to those that did not die in traps, and included interactions among capture number, mortality, and age and sex, respectively. We excluded all notably pregnant females from analyses.

RESULTS

We captured 806 deer mice, 152 red-backed voles, and 126 red-tailed chipmunks 2 or more times. Body mass declined significantly over successive captures for deer mice ($F = 66.30$; $df = 1, 1,194$; $P < 0.001$), red-backed voles ($F = 4.74$; $df = 1, 279$; $P = 0.030$), and red-tailed chipmunks ($F = 12.92$; $df = 1, 219$; $P < 0.001$; Fig. 1).

Juveniles generally exhibited less severe declines in mass than adults. At second and third captures,

juvenile deer mice showed evidence of relatively small mass declines and juvenile red-backed voles and red-tailed chipmunks demonstrated mass increases (Fig. 2). This age distinction is evident in the significant interaction between capture and age for deer mice ($F = 35.8$; $df = 1, 1,992$; $P < 0.001$), red-backed voles ($F = 8.86$; $df = 1, 277$; $P = 0.003$), and red-tailed chipmunks ($F = 4.29$; $df = 1, 217$; $P = 0.040$). When we evaluated age classes in separate models, juveniles of all 3 species showed nonsignificant changes in mass ($P > 0.35$), whereas adults showed strong declines ($P < 0.001$).

Female red-backed voles differed from males in that they tended to maintain their body mass while males exhibited mass declines ($F = 7.78$; $df = 1, 277$; $P = 0.006$). However, mass change did

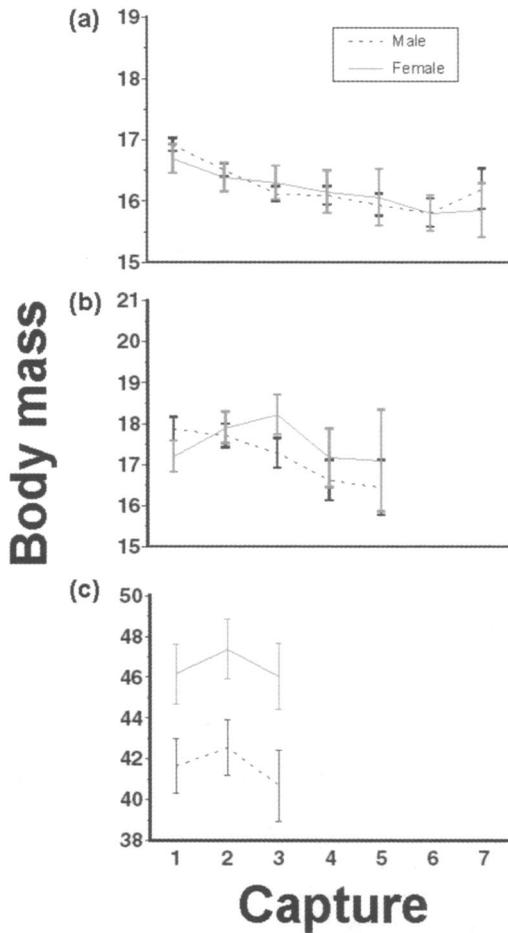


Fig. 3. Changes in body mass (g) with repeated captures presented as adjusted means (\pm SE) for male versus female (a) deer mice, (b) red-backed voles, and (c) red-tailed chipmunks live-trapped in Montana, USA, 1996 and 1997.

not differ by sex in deer mice ($F = 1.43$; $df = 1, 1,192$; $P = 0.232$) or red-tailed chipmunks ($F = 0.05$; $df = 1, 217$; $P = 0.816$; Fig. 3).

Length of rest intervals between recaptures significantly reduced mass declines for deer mice ($F = 5.06$; $df = 1, 1,189$; $P = 0.025$; Fig. 4), but not for red-backed voles ($F = 0.03$; $df = 1, 123$; $P = 0.864$) or red-tailed chipmunks ($F = 0.54$; $df = 1, 90$; $P = 0.465$). Relationships between rest intervals and mass change did not differ by age or sex for deer mice (age: $F = 0.28$; $df = 1, 1,189$; $P = 0.595$; sex: $F = 0.69$; $df = 1, 1,189$; $P = 0.405$), red-backed voles (age: $F = 0.3$; $df = 1, 123$; $P = 0.584$; sex: $F = 0.71$; $df = 1, 123$; $P = 0.402$), or red-tailed chipmunks (age: $F = 0.18$; $df = 1, 90$; $P = 0.671$; sex: $F = 0.83$; $df = 1, 90$; $P = 0.364$).

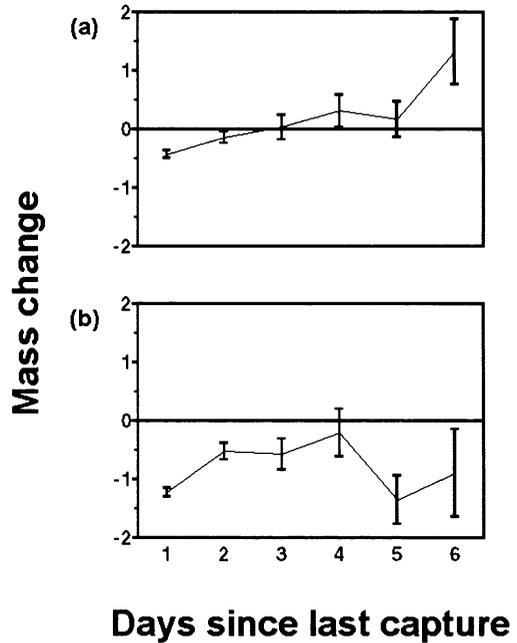


Fig. 4. Mean (\pm SE) change in body mass (g) as a function of rest interval between captures for (a) juvenile and (b) adult deer mice live-trapped in Montana, USA, 1996 and 1997.

Animals that died in traps exhibited greater mass declines than those that survived for deer mice ($F = 42.03$; $df = 1, 1,989$; $P < 0.001$), but differences were not significant for red-backed voles ($F = 2.69$; $df = 1, 274$; $P = 0.102$) or red-tailed chipmunks ($F = 0.24$; $df = 1, 214$; $P = 0.624$; Fig. 5). The relationship between mortality and mass change differed between age classes for deer mice ($F = 17.03$; $df = 2, 1,989$; $P < 0.001$) and red-backed voles ($F = 4.59$; $df = 2, 274$; $P = 0.011$), but not for red-tailed chipmunks ($F = 2.41$; $df = 2, 214$; $P = 0.092$). Juvenile deer mice that died in traps exhibited drastic mass declines relative to surviving juveniles, whereas adults that died tended to exhibit comparable declines to those that did not. Conversely, adult red-backed voles that died in traps showed greater mass declines than those that did not, whereas juveniles that died showed less pronounced differences in mass change than those that survived. Mortality effects differed by sex for red-backed voles ($F = 3.43$; $df = 2, 274$; $P = 0.033$), but not for deer mice ($F = 0.64$; $df = 2, 1,989$; $P = 0.528$) or red-tailed chipmunks ($F = 1.23$; $df = 2, 214$; $P = 0.294$). Both male and female red-backed voles that died in traps exhibited strong declines relative to surviving

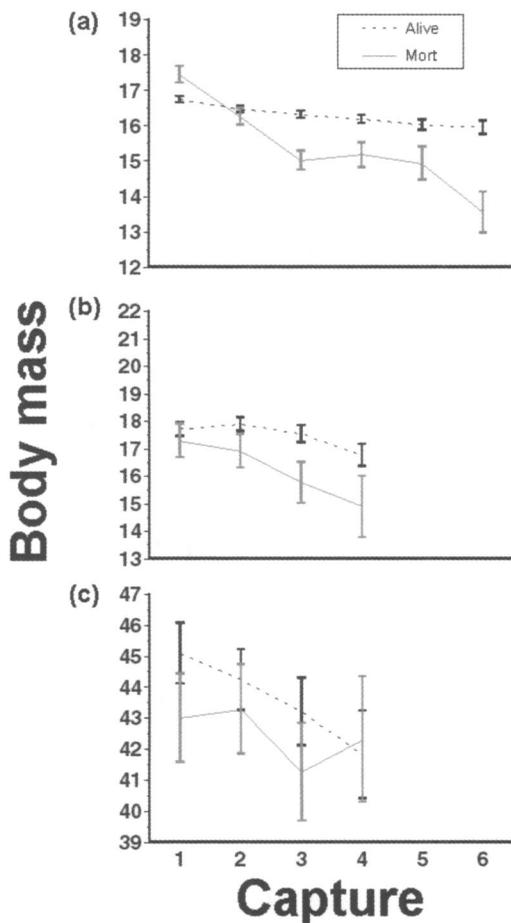


Fig. 5. Changes in body mass (g) with repeated captures presented as adjusted means (\pm SE) for (a) deer mice, (b) red-backed voles, and (c) red-tailed chipmunks found dead versus those found alive in traps in Montana, USA, 1996 and 1997.

individuals, but females that survived trapping tended to increase in mass, whereas males that survived showed moderate decreases in mass.

DISCUSSION

Body mass is an important indicator of survival and fecundity (McClenaghan and Gaines 1978, Myers and Master 1983, Sauer and Slade 1986) that is commonly used as an index of habitat quality and population health (e.g., Albers et al. 1990, Peles and Barrett 1996, Von Trebra et al. 1998). Therefore, if sampling methods such as live-trapping reduce body mass before it can be measured, measures of body mass will be negatively biased indices of true mass. Although a negatively biased index can be used for relative com-

parisons so long as the bias remains reasonably constant (McKelvey and Pearson 2001), if the bias differs among study populations, then observed differences in body mass may reflect differential bias rather than actual differences in the parameter of interest. Moreover, if repeated captures cause cumulative mass declines, then mass declines could result in reduced survival and fitness of study populations, thereby confounding attempts to quantify population attributes.

We found that body masses declined over successive captures for deer mice, red-backed voles, and red-tailed chipmunks. Similar body mass declines have been described for naked-soled gerbils (*Tatera brantsii* and *T. leucogaster*) in Africa (Korn 1987), for wood mice (*Apodemus sylvaticus*) and bank voles (*Clethrionomys glareolus*) in Europe (Korn 1987, Schon and Korn 1992), and for hispid cotton rats (*Sigmodon hispidus*), meadow voles (*Microtus pennsylvanicus*), deer mice, and prairie voles (*M. ochrogaster*) in North America (Bietz et al. 1977, Slade and Iskjaer 1990, Slade 1991, Kaufman and Kaufman 1994). The fact that live-trapping is the single common factor linking small-mammal studies reporting mass declines for a diversity of taxa from a wide range of environments indicates that mass declines are a trap-induced phenomenon. The consistency with which losses of mass experienced by small mammals increases with repeated captures indicates that trapping effects are cumulative. We refer to this phenomenon of cumulative mass declines from repeated captures as TMD.

Cumulative effects of trapping are likely to result in reduced vigor and fitness for individuals as recaptures accumulate. Such effects are difficult to quantify directly, but extreme cases may manifest themselves as trap mortality. Although many authors have raised concerns regarding trap mortality, most discussions treat trap death as a discrete event that results from a particular set of environmental conditions such as high temperatures (Schon and Korn 1992, Kaufman and Kaufman 1994) or low temperatures in combination with moisture (Corke 1967, Perrin 1975, Gurnell 1982) that induce mortality during a single capture period. Such single-event mortalities certainly occur, but cumulative mass declines brought about by trapping are likely to result in depressed body masses and associated physiological conditions that weaken animals to such an extent that they ultimately die either within the trap or after release.

We tested the hypothesis that TMDs incur trap mortality by comparing mass declines in animals that died in traps with those that did not. Mass

declines associated with animals that died in traps tended to be more severe than mass declines associated with trap survivors for all species, but differences were significant only for deer mice. Our results suggest that TMDs may result in trap mortality, and that this condition can vary by species and demographic group.

Research has shown that body mass is correlated with survival (Myers and Master 1983, McClenaghan and Gaines 1978, Sauer and Slade 1986). Therefore, some animals that exhibit large TMDs and do not die in traps, likely die soon after release, either from the immediate effects of mass reductions or from increased susceptibility to predation, starvation, exposure, or other factors. In addition, animals that do not die from TMDs may still exhibit reduced fitness as body mass is related to fecundity (Myers and Master 1983).

Kaufman and Kaufman (1994) concluded that trap effects measured for deer mice were short-term, but the authors did not address repeated captures. Perrin (1975) argued that trap deaths of field voles (*Microtus agrestis*) and bank voles were not associated with repeated captures, but he discounted the significant losses in mass already incurred by the first 2 captures (e.g., Kaufman and Kaufman 1994) by lumping the first and second captures. Slade (1991) reported that hispid cotton rats quickly regained mass lost during trapping, and concluded that mass declines were only short-term in this species and did not affect survival. However, he found that individual prairie voles that lost the most mass within a trapping period also lost the most or regained the least mass between trapping periods, suggesting long-term impacts of mass declines. Slade's (1991) results in conjunction with ours suggest that TMDs may reduce fitness in some live-trapped small-mammal populations, thereby causing demographic impacts that extend beyond the immediate trapping session.

Numerous studies have described significant TMDs in spite of the rest intervals that commonly occur between captures, but we found no studies that considered the influence of rest intervals on mass declines. Our results demonstrate that the severity of TMDs can be reduced by longer rest intervals for deer mice, suggesting that methods involving pulse-trapping (e.g., Pollock's robust design [Pollock 1982]) might reduce trap effects for some species. However, for other species such as red-backed voles and red-tailed chipmunks, rest intervals between captures did not appear to alleviate mass declines even over 8-day trapping

sessions, which allowed for relatively long rest intervals between captures (up to 6 days).

We found that TMDs also varied among age and sex classes. Juveniles exhibited less severe mass declines than adults for all 3 species. Whereas adults showed strong, consistent mass declines with repeated captures, juveniles did not. For juveniles, mass change was variable across capture number but showed some evidence of increase relative to adults despite trapping effects. Slade (1991) and Kaufman and Kaufman (1994) similarly reported that younger, more rapidly growing age classes suffered smaller mass losses than older age classes. Bietz et al. (1977) observed no differences in mass losses between age classes of meadow voles, but this may partly result from the fact that they compared adults versus subadults rather than adults versus juveniles. Differences in TMDs between age classes suggest that juvenile growth rates partly offset TMDs. However, this does not mean that juveniles are less impacted by TMDs, as juveniles would be expected to increase in mass. Trap-mortality studies suggest that juveniles are more sensitive to trap stress than adults (Drickamer and Paine 1992).

We observed differences in TMDs between sexes for red-backed voles, but not for other species. Others have also reported variable results with regard to sex. Bietz et al. (1977) reported no difference in mass losses between male and female *M. pennsylvanicus*, but Slade (1991) reported that adult female *S. hispidus* and *M. ochrogaster* gained mass in spring while males lost mass, and Kaufman and Kaufman (1994) found that female deer mice lost more mass than males in the spring. These apparently contradictory results likely reflect the timing of sampling relative to the phenology of breeding in females. Growth of fetuses may offset mass declines, but when parturition occurs between captures, females may appear to experience greater mass declines. We conducted our trapping during the spring breeding season, and although we excluded all notably pregnant females from analyses, the observed tendency of females to lose less mass than males may reflect undetected pregnancies. Measured differences in female body mass among populations (e.g., Albers et al. 1990, Kaufman and Kaufman 1994, Peles and Barrett 1996) may be more indicative of reproductive differences (as noted by Peles and Barrett 1996) than actual differences in body mass. This being the case, males should provide a better measure of differences in body mass between populations.

Our data do not address the causes of TMDs, but field and laboratory studies suggest that cold, wet conditions leading to hypothermia and hot, dry conditions leading to dehydration may cause trap mortality (Perrin 1975, Gurnell 1982, Schon and Korn 1992, Kaufman and Kaufman 1994). Trap designs may mediate some of these effects (Llewellyn 1950), but studies reporting mass declines have included Sherman, Longworth, modified Fitch, and multi-capture wooden traps (e.g., Brown 1973, Bietz et al. 1977, Slade 1991). Comparisons of trap bait have produced variable results but generally suggest that moist foods such as apples or potatoes may reduce trap stress from dehydration (Llewellyn 1950, Schon and Korn 1992). Schon and Korn (1992) showed that mass losses in *C. glareolus* were not reduced by the availability of nest boxes, but were reduced by offerings of apples, suggesting that nesting conditions were not as important as moist foods for alleviating mass declines.

Although we did not use bedding material in our traps, mass declines have been commonly reported by researchers using bedding materials (Bietz et al. 1977, Slade 1991, Kaufman and Kaufman 1994). Surprisingly, we found no studies examining the effects of bedding material on TMDs or trap mortality. Research is necessary to assess the efficacy of bedding material for reducing trapping effects on small mammals, given that handling soiled bedding material could increase the risk for humans of contracting Hantavirus pulmonary syndrome (Childs et al. 1994) and other zoonotic diseases.

We found that mass declines differed among species and demographic groups. Further evidence indicates that TMDs can be induced by dehydration (Schon and Korn 1992, Kaufman and Kaufman 1994), a physiological condition that will vary by environment. Therefore, comparisons of body mass measures among species, demographic groups, or environmental conditions that differentially affect TMDs are subject to differential bias of the index. For example, if dehydration causes TMDs, animals trapped in uncut, mature forests may exhibit less severe TMDs than animals captured in comparable recently clearcut forests because of increased solar radiation. Therefore, observing significantly higher small-mammal body mass in habitats with greater vegetative cover may reflect a bias in trap effects rather than differences in the relative quality of the environments. This point is emphasized by the fact that differences in body mass observed between habitats for *Peromyscus*, *Clethrionomys*,

and *Microtus* (Albers et al. 1990, Peles and Barrett 1996, Von Trebra et al. 1998) are comparable to TMDs described here and elsewhere (Brown 1973, Korn 1987, Kaufman and Kaufman 1994).

Restricting body mass comparisons to first captures will reduce the effect of TMDs on measures of body mass (Slade and Iskjaer 1990), but will not alleviate the bias. Kaufman and Kaufman (1994) showed that deer mice had already lost significant mass at the first capture based on precapture masses from nest boxes. Researchers wanting to compare body mass among species, demographic groups within species, or populations exposed to different environmental conditions that might affect TMDs should consider correcting the index or testing for differential bias. Regressions constructed from recapture data could be used to back calculate the mean precapture mass based on the assumption that the process of body mass decline is linear and extends through the first capture. Alternatively, one could compare the slopes of the regression lines between samples of interest to test for differences in the process of mass declines between populations. If no differences are found, first capture mass could be used under the assumption that no evidence exists of differential bias. However, both methods are heavily dependent upon recapture data. Therefore, large samples and high recaptures are necessary to be effective, and the question of whether the bias adjustment effectively improves the index should be considered (McKelvey and Pearson 2001).

MANAGEMENT IMPLICATIONS

Assessing habitat quality and monitoring population health is integral to managing wildlife populations, yet indices used to quantify these important attributes can sometimes be misleading (e.g., Van Horne 1983). Body mass is an important biological attribute that is commonly used to assess population health and habitat quality. However, our results indicate that standard sampling procedures such as live-trapping can cause body mass declines, thereby rendering measures of body mass negatively biased indices that can differ by species, demography, and habitat. Ignoring this bias can result in misinterpreting observed differences in body mass as differences in population health or habitat quality. Thus, use of live-trapping to index body mass should be avoided when differential bias is suspected, or the bias should be corrected.

Our results also suggest that cumulative effects of TMDs may cause trap mortality and otherwise reduce the vigor of populations under study. Such

observer effects can interfere with other research and monitoring goals such as population and survivorship estimation, because estimating these parameters depends heavily on recapture data associated with longer sampling periods (e.g., White et al. 1982). Population and survivorship estimation approaches based on trapping designs that incorporate rest periods (e.g., Pollock 1982) may reduce this problem, since rest intervals between captures appear to reduce TMDs in some species. Additional research is necessary to determine the precise causes of TMDs.

ACKNOWLEDGMENTS

We thank K. R. Foresman, R. M. King, and J. R. Waters for helpful reviews on earlier manuscripts. R. M. King and D. L. Turner advised on data analysis. D. Lockman and C. Stewart directed us in locating study sites. We commend our field crews, A. Edmonds, E. Holt, J. Kolbe, L. Krigbaum, E. Lindberg, T. Musci, and A. Stanley for their dedication to collecting quality data. Funding was provided by the U.S. Department of Agriculture Forest Service, Bitterroot Ecosystem Management Research Project, and the Wildlife Ecology Research Unit of the Rocky Mountain Research Station, Missoula, Montana, USA.

LITERATURE CITED

- ALBERS, P. H., G. LINDER, AND J. D. NICHOLS. 1990. Effects of tillage practices and carbofuran exposure on small mammals. *Journal of Wildlife Management* 54:135–142.
- BIETZ, B. F., P. H. WHITNEY, AND P. K. ANDERSON. 1977. Weight loss of *Microtus pennsylvanicus* as a result of trap confinement. *Canadian Journal of Zoology* 55:426–429.
- BROWN, E. B., III. 1973. Changes in patterns of seasonal growth of *Microtus pennsylvanicus*. *Ecology* 54:1103–1110.
- CHILDS, J. E., T. G. KSIAZEK, C. F. SPIROPOULOU, J. W. KREBS, S. MORZUNOV, G. O. MAUPLIN, K. L. GAGE, P. E. ROLLIN, J. SARISKY, R. E. ENSCORE, J. K. FREY, C. J. PETERS, AND S. T. NICHOL. 1994. Serologic and genetic identification of *Peromyscus maniculatus* as the primary rodent reservoir for a new Hantavirus in the southwestern United States. *Journal of Infectious Diseases* 169:1271–1280.
- CORKE, D. 1967. The deaths of small mammals in live-traps. *Journal of Zoology* 153:552.
- DRICKAMER, L. C., AND C. R. PAINE. 1992. Sex, age, nest construction and trap mortality for six species of rodents. *American Midland Naturalist* 128:360–365.
- GURNELL, J. 1982. Trap deaths in woodland rodents. *Acta Theriologica* 27:139–147.
- KAUFMAN, G. A., AND D. W. KAUFMAN. 1994. Changes in body mass related to capture in the prairie deer mouse (*Peromyscus maniculatus*). *Journal of Mammalogy* 75:681–691.
- KORN, H. 1987. Effects of live-trapping and toe-clipping on body weight of European and African rodent species. *Oecologia* 71:597–600.
- LLEWELLYN, L. M. 1950. Reduction of mortality in live-trapping mice. *Journal of Wildlife Management* 14:84–85.
- MCCLENAGHAN, L. R., JR., AND M. S. GAINES. 1978. Reproduction in marginal populations of the hispid cotton rat (*Sigmodon hispidus*) in northeastern Kansas. *Occasional Papers Museum of the Natural History Museum, The University of Kansas* 74:1–16.
- McKELVEY, K. S., AND D. E. PEARSON. 2001. Population estimation with sparse data: the role of indices versus estimators revisited. *Canadian Journal of Zoology* 79:1754–1765.
- MILLS, J. N., T. L. YATES, J. E. CHILDS, R. R. PARMENTER, T. G. KSIAZEK, P. E. ROLLIN, AND C. J. PETERS. 1995. Guidelines for working with rodents potentially infected with Hantavirus. *Journal of Mammalogy* 76:716–722.
- MYERS, P., AND L. L. MASTER. 1983. Reproduction by *Peromyscus maniculatus*: size and compromise. *Journal of Mammalogy* 64:1–18.
- NUPP, T. E., AND R. K. SWIHART. 1998. Effects of forest fragmentation on population attributes of white-footed mice and eastern chipmunks. *Journal of Mammalogy* 79:1234–1243.
- PELES, J. D., AND G. W. BARRETT. 1996. Effects of vegetative cover on the population dynamics of meadow voles. *Journal of Mammalogy* 77:857–869.
- PERRIN, M. R. 1975. Trap deaths. *Acta Theriologica* 20:167–174.
- POLLOCK, K. H. 1982. A capture–recapture design robust to unequal probability of capture. *Journal of Wildlife Management* 46:752–757.
- SAS INSTITUTE. 1999. Proc mixed. Version 8.1 for AIX. SAS Institute, Cary, North Carolina, USA.
- SAUER, J. R., AND N. A. SLADE. 1986. Field-determined growth rates of prairie voles (*Microtus ochrogaster*): observed patterns and environmental influences. *Journal of Mammalogy* 67:61–68.
- SCHON, I., AND H. KORN. 1992. Causes and magnitude of body weight changes in trap-confined bank voles, *Clethrionomys glareolus*. *Journal of Zoology* 227:319–325.
- SLADE, N. A. 1991. Loss of body mass associated with capture of *Sigmodon* and *Microtus* from northeastern Kansas. *Journal of Mammalogy* 72:171–176.
- , AND C. ISKJAER. 1990. Daily variation in body mass of free-living rodents and its significance for mass-based population dynamics. *Journal of Mammalogy* 71:357–363.
- SULLIVAN, T. P., C. NOWOTNY, R. A. LAUTENSCHLAGER, AND R. G. WAGNER. 1998. Silvicultural use of herbicide in sub-boreal spruce forest: implications for small mammal population dynamics. *Journal of Wildlife Management* 62:1196–1206.
- VAN HORNE, B. 1983. Density as a misleading indicator of habitat quality. *Journal of Wildlife Management* 47:893–901.
- VON TREBRA, V. C., D. P. LAVENDER, AND T. S. SULLIVAN. 1998. Relations of small mammal populations to even-aged shelterwood systems in sub-boreal spruce forest. *Journal of Wildlife Management* 62:630–642.
- WHITE, G. C., D. R. ANDERSON, K. P. BURNHAM, AND D. L. OTIS. 1982. Capture-recapture and removal methods for sampling closed populations. Los Alamos National Laboratory, Los Alamos, Texas, USA.

Received 22 August 2002.

Accepted 1 July 2003.

Associate Editor Russell.