(1427)

Differences in trapping mortality rates of northern flying squirrels

DANIEL K. ROSENBERG[1] AND ROBERT G. ANTHONY

U.S. Fish and Wildlife Service (RGA), Oregon Cooperative Wildlife Research Unit, Department of Fisheries and Wildlife, Oregon State University, Corvallis, OR 97331, U.S.A.

Received July 27, 1992
Accepted October 27, 1992

ROSENBERG, D. K., and ANTHONY, R. G. 1993. Differences in trapping mortality rates of northern flying squirrels. Can. J. Zool. **71**: 660–663.

We described trapping mortality rates of northern flying squirrel (*Glaucomys sabrinus*) populations in western Oregon, U.S.A., and evaluated the effects of sex, age, body mass, and number of times an individual was recaptured on these rates. Although the overall trapping mortality rates were relatively low (7%) during 16–21 day trapping sessions, we observed differential mortality rates among the sex and age cohorts. The order of mortality rates was: juvenile females (32.3%) > juvenile males (11.1%) > adult females (5.1%) = adult males (4.1%). Overall trapping mortality rates were not affected by the number of times an individual was captured. We hypothesize that the differences we found were due to extrinsic factors (weather-related) acting on differential behavioral responses to trapping and thresholds of stress an animal can tolerate.

ROSENBERG, D. K., et ANTHONY, R. G. 1993. Differences in trapping mortality rates of northern flying squirrels. Can. J. Zool. **71** : 660–663.

Nous avons déterminé les taux de mortalité au piégeage dans des populations du Petit Polatouche (*Glaucomys volans*) de l'ouest de l'Orégon, U.S.A. et évalué les effets du sexe, de l'âge, de la masse et du nombre de recaptures sur cette mortalité. Bien que le taux de mortalité global au piégeage ait été assez bas (7%) au cours de périodes de piégeage de 16 à 21 jours, les taux variaient d'après le sexe et l'âge. La mortalité décroissait de 32,3% chez les jeunes femelles à 11,1% chez les jeunes mâles, à 5,1% chez les femelles adultes et à 4,1% chez les mâles adultes. Il n'y avait pas de relation entre le nombre de fois qu'un individu était recapturé et la mortalité globale. Nous croyons que les différences que nous avons observées sont dues à des facteurs extrinsèques (réliés au climat) agissant sur les réactions comportementales variables au piégeage et sur les niveaux de stress que chaque animal peut supporter.

[Traduit par la rédaction]

Introduction

Live trapping is often used to study population characteristics of mammals. Although the intent is for animals to survive this process, some may not. Animals that die may not be representative of the population, because sex, age, body mass, and previous trapping history may affect mortality among trapped animals (trapping mortality) (Perrin 1975; Montgomery 1980; Gurnell 1982).

Differential trapping mortality may affect recruitment, immigration, and emigration rates by altering the proportion of

[1]Author to whom all correspondence should be addressed.

Printed in Canada / Imprimé au Canada

TABLE 1. Trapping mortality and body mass of northern flying squirrels that survived or died in traps in western Oregon, autumn 1988–1990

	Males						Females					
	Survived			Died			Survived			Died		
		Body mass (g)			Body mass (g)			Body mass (g)			Body mass (g)	
Age-class	N	$\bar{X}$	SE	N	$\bar{X}$	SE	N	$\bar{X}$	SE	N	$\bar{X}$	SE
Juvenile[a]	64	92.2	1.0	8	92.0	3.0	44	93.4	1.1	21	92.7	1.8
Adult[b]	254	130.2	0.9	11	128.4	4.6	315	134.4	0.9	17	135.8	4.5

[a]Squirrels with body mass < 104 g.
[b]Squirrels with body mass ≥ 104 g.

individuals in each sex and age-class. The proportion of juveniles entering the cohort of reproducing animals may be a critical factor affecting population dynamics, especially in populations with high adult mortality rates. Similarly, sex ratios of populations may play important roles in regulating population size.

Although trapping mortality is common in mark–recapture studies, few researchers have compared characteristics of animals that died with those of the population. Trapping mortality has been reported to vary among mammal species (Platt 1968), seasons (Gurnell 1982), age (Perrin 1975; Montgomery 1980; Gurnell 1982), and previous trapping history (Montgomery 1980; Gurnell 1982). Understanding the degree of vulnerability of each segment of the population is important for predicting the consequence of trapping mortality on the population structure. We report differences in trapping mortality among age- and sex-classes, and in relation to the number of times each individual was captured in populations of northern flying squirrels (*Glaucomys sabrinus*).

Methods and materials

We trapped flying squirrels in 10 coniferous forest stands on the west slope of the Cascade Range in the Blue River and McKenzie River Ranger Districts, Willamette National Forest, near the towns of Blue River and McKenzie Bridge, Lane County, Oregon, U.S.A. Stands were at elevations between 375 and 900 m, and slope ranged from 10 to 60%. Climate in the region of the study area is characterized by mild wet winters and warm dry summers (Franklin and Dyrness 1973). Details of stand characteristics are described elsewhere (Rosenberg and Anthony 1992).

In each stand we established a 13-ha live-trapping grid consisting of 96–100 trap stations spaced 40 m apart. Grid arrays varied from 10 × 10 to 16 × 6 trap stations, depending on the size and shape of stands. Two Tomahawk No. 201 (41 × 13 × 13 cm) live traps (Tomahawk Live Trap Co., Tomahawk, Wisconsin) were placed at each station. One trap was placed approximately 1.5 m above ground in the largest tree, within 5 m of the trap station; the second trap was placed on the ground within 2 m of the tree (Witt 1991). Traps were baited with a mixture of peanut butter, whole oats, molasses, and a high protein (>30%) pellet. A nest box with polyester batting was placed near the rear of the trap. Squirrels were ear-tagged with monel No. 1 tags (National Band and Tag Co., Newport, Kentucky), and body mass and sex were recorded at first capture each year. We trapped on 10 grids once each year in 1988 and 1989, and on 5 grids in 1990. All trapping was done during October and November for 16–21 consecutive nights.

The lowest body mass of squirrels recaptured 1 year after their initial capture (N = 175) was 104 g (Rosenberg and Anthony 1992); therefore, animals weighing less than this were considered juveniles. We classified squirrels ≥104 g as "adults," but this weight class may include juveniles (Davis 1963, pp. 8, 53).

TABLE 2. Comparison of the probability of trap death of northern flying squirrels among different age and sex classes, Willamette National Forest, Oregon, autumn 1988–1990

	Proportional difference of probability of death[a]	
Age and sex classes	Ratio	95% CI
Adult female/adult male	1.2	0.6–2.7
Juvenile female/adult male	11.0	5.0–24.4*
Juvenile female/adult female	8.8	4.3–18.0*
Juvenile male/adult male	2.9	1.1–7.5*
Juvenile female/juvenile male	3.8	1.5–9.4*

NOTE: Significance tests are from the logistic regression model $\ln[P/(1-P)] = B_0 + B_1$ (age) + B_2 (sex) + B_3 (age × sex) where P is the probability of death. 95% CI, 95% confidence interval.
[a]Ratios of 1.0 indicate an equal likelihood of death; confidence intervals that do not include 1.0 indicate an unequal likelihood of death (*, $P \leq 0.05$).

We used logistic regression to evaluate whether mortality varied among age and sex classes. We pooled the data from all 3 years because of small sample sizes in each year. From the logistic model that best fit the data ($\ln[P/(1-P)] = B_0 + B_1$ (age) + B_2 (sex) + B_3 (age × sex), where P is the probability of death), we calculated the probability of death for the various sex and age groups and report both the probability and its confidence interval. Body mass was compared between the sexes and between those that died during or survived (i.e., observed alive in traps) trapping with two-way analysis of variance for juveniles and adults, separately. We used χ^2 contingency tests to determine whether the number of times an individual was captured (1, 2, 3, 4, and ≥5 times) during the 16- to 21-day trapping period differed between squirrels that died and those that survived. Age, sex, and years were pooled for these analyses because of small sample sizes in some groups, and after finding no significant differences (χ^2 = 1.0, df = 3, $P > 0.7$) among age and sex classes.

Results

We recorded body mass and sex for 734 of the 765 flying squirrels captured. Fifty-seven squirrels (7.5%) died during trapping. Trapping mortality was not random with respect to age and sex (Table 1). The probability of death was affected by age ($P = 0.03$) and by the interaction of age and sex ($P = 0.06$). Sex, without considering interaction with age, was not significant ($P = 0.6$; Table 2). Juvenile squirrels had significantly higher trapping mortality rates (21.2%) than the adults (4.7%; Table 2). Although the mortality rates for adult females (5.1%) and adult males (4.1%) were comparable, juvenile females had significantly higher rates (32.3%) than juvenile males (11.1%; Table 2).

In the trapped population, body mass was greater for adult

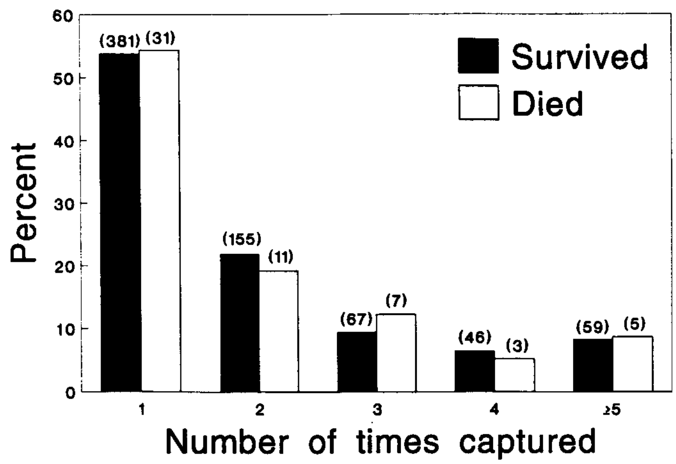

FIG. 1. Percentage of flying squirrels that survived ($N = 708$) and those that died ($N = 57$) during trapping in relation to the number of times they were captured. Numbers in parentheses are the sample sizes.

females ($\bar{X} \pm$ SE, 134 $\pm$ 0.9 g, $N = 332$) than for adult males (130 $\pm$ 0.9 g, $N = 265$; $F = 11.0$, $P = 0.001$), but there was no difference in mass between juvenile females (93 $\pm$ 0.9 g, $N = 65$) and juvenile males (92 $\pm$ 1.0 g, $N = 72$; $F = 0.5$, $P = 0.5$). There was no significant difference in body mass between squirrels that died in traps and those that survived (juveniles: $F = 0.02$, $P = 0.9$; adults: $F = 0.01$, $P = 0.9$; Table 1).

More than half of the squirrels were captured only once, for both those that survived (381 of 708, 53.8%) and for those that died (31 of 57, 54.4%) during the trapping session. There was no significant difference in the number of times an individual was captured between these two groups ($\chi^2 = 0.7$, df = 1, $P > 0.25$; Fig. 1).

Discussion

We found differential trapping mortality within populations of northern flying squirrels in western Oregon during our study. Adult mortality rates reported here are probably biased high because some juveniles reach adult weight by autumn (Davis 1963, p. 53) and would have been assigned to the adult class. If this is the case, then the differences between adults and juveniles are even greater than suggested by the data. The number of times an individual was captured did not affect the trapping mortality of northern flying squirrels. Similar observations were made on bank voles (*Clethrionomys glareolus*) and European field voles (*Microtus agrestis*) (Perrin 1975; Montgomery 1980).

The few investigators that have reported comparisons of trapping-mortality rates among age and sex classes suggested that a variety of responses occur. For example, juvenile bank voles experienced higher rates of trapping mortality than adults (Montgomery 1980; Gurnell 1982), and individuals with lower body mass tended to have higher mortality rates (Perrin 1975); however, sample sizes used in the analyses were small. Breeding condition may also influence trapping-mortality rates; breeding female bank voles and wood mice (*Apodemus sylvaticus*) had higher rates than nonbreeding females or males (Gurnell 1982).

Reasons for the disproportionately high mortality rate in juveniles, particularly juvenile females, are unknown. Differences in carbohydrate reserves could be important because trap deaths may result from hypoglycemia (Guthrie et al. 1967; Keith et al. 1968). Fat reserves may be proportionately greater in adult than in juvenile flying squirrels, as is generally true with mammals (Pond 1981). Carbohydrates consumed in autumn may be allocated to accumulation of fat in adult squirrels (Witt 1991) whereas juvenile squirrels would be expected to allocate more energy to growth than to fat reserves.

The difference in carbohydrate reserves may be a valid hypothesis for the difference in adult and juvenile mortality rates, but it does not explain the higher trapping-mortality rates among females within the juvenile cohort. Because body mass was similar for juvenile males and females, a behavioral rather than a strictly physiological explanation may be more realistic. Unfortunately, our data would not provide a test of this hypothesis. Laboratory studies of differential thresholds of stress, similar in methodology to Rock and Williams (1979), would be necessary for such a test.

Extrinsic factors, such as temperature and precipitation, acting on animals in poor physiological condition were suggested as causes of differential trap mortality (Perrin 1975; Gurnell 1982). This dual hypothesis (extrinsic and intrinsic factors) may account for the differences we observed as well as those in the previous studies mentioned. In addition to physiological condition, differential behavioral response to trapping and the thresholds of stress an animal can tolerate could be important intrinsic factors.

Regardless of the causal factors for the patterns we found, there are implications for population studies of animals where live-trapping techniques are used. Characteristics of populations within a study area could be affected by changes in the age composition and the sex ratio of the juvenile cohort, especially for populations that are trapped during long-term studies. Comparisons of populations may also be biased by differential mortality if patterns of trapping deaths are not recognized.

The effect that differential trapping mortality has on the population under study would depend on the immigration of animals from the surrounding areas, natural mortality and emigration rates, and whether trapping mortality is compensatory or additive. For example, in the flying squirrel populations we examined the percentage of individuals recaptured a year after their initial capture ranged from 21 to 50% (Rosenberg and Anthony 1992) which suggests a relatively high turnover rate due to either emigration or mortality. Therefore, the age- and sex-specific trapping-mortality rate we observed may not have affected the population to the same extent had natural mortality and emigration rates been low.

Mark–recapture methods used to estimate abundance and survival rates perform best with high recapture rates (Otis et al. 1978; Pollock et al. 1990). In order to reliably estimate these parameters, a large number of trapping attempts may be required for populations that exhibit low capture probabilities (Otis et al. 1978), such as the squirrel populations we studied (Rosenberg 1991). Although mortality rates did not seem to be affected by repeated capture, over 40% of trapping deaths occurred after the first capture. Fewer deaths would have occurred had animals not been recaptured, but less reliable parameter estimates would have resulted. Investigators should consider both how trapping effort affects the population characteristics being studied, and the need to obtain reliable estimates.

Acknowledgements

We thank G. S. Miller for his help with the location of study sites and logistical coordination, D. A. DellaSala for contributing to the study design, and M. T. Brown and K. A. Swindle for coordinating the 1989 and 1990 trapping sessions, respectively; and S. K. Albert, G. M. Bennett, T. Brown, T. D. Buchholz, D. DellaSala, S. M. Desimone, M. Fishman, J. D. Hall, M. C. Hansen, B. C. Latta, R. S. Lutz. N. V. Marr, G. Orth, K. A. Swindle, and M. Vander Heyden for their valuable contributions to the trapping effort; the staff at H. J. Andrews Experimental Forest for providing accommodations, and L. Alexander, K. B. Aubry, S. M. Desimone, S. DeStefano, C. Maguire, R. J. Steidl, K. A. Swindle, and J. R. Waters for helpful comments on a draft of the manuscript. S. Harmsen provided helpful insights into the statistical methods used. Funding was provided by the U.S. Forest Service, Pacific Northwest Research Station, Olympia, Washington, to the Oregon Cooperative Wildlife Research Unit. Cooperators included the U.S. Fish and Wildlife Service, Oregon State University, Oregon Department of Fish and Wildlife, and the Wildlife Management Institute. Analysis and manuscript preparation were done while the senior author was employed by the U.S. Forest Service, Redwood Sciences Laboratory, Arcata, California.

Davis, W. 1963. Reproductive ecology of the northern flying squirrel in Saskatchewan. M.A. thesis, Department of Biology, University of Saskatchewan, Saskatoon.

Franklin, J. F., and Dyrness, C. T. 1973. Natural vegetation of Oregon and Washington. USDA For. Serv. Gen. Tech. Rep. PNW-8.

Gurnell, J. 1982. Trap deaths in woodland rodents. Acta Theriol. **27**: 139–147.

Guthrie, D. R., Osborne, J. C., and Mosby, H. S. 1967. Physiological changes associated with shock in confined gray squirrels. J. Wildl. Manage. **31**: 102–108.

Keith, L. B., Meslow, E. C., and Rongstad, O. J. 1968. Techniques for snowshoe hare population studies. J. Wildl. Manage. **32**: 801–812.

Montgomery, W. I. 1980. Mortality of small rodents captured in live-traps. Acta Theriol. **25**: 277–294.

Otis, D. L., Burnham, K. P., White, G. C., and Anderson, D. R. 1978. Statistical inference from capture data on closed animal populations. Wildl. Monogr. No. 62.

Perrin, M. R. 1975. Trap deaths. Acta Theriol. **20**: 167–174.

Platt, A. P. 1968. Differential trap mortality as a measure of stress during times of population increase and decrease. J. Mammal. **49**: 331–335.

Pollock, K. H., Nichols, J. D., Brownie, C., and Hines, J. D. 1990. Statistical inference for capture–recapture experiments. Wildl. Monogr. No. 107.

Pond, C. M. 1981. Storage. *In* Physiological ecology: an evolutionary approach to resource use. *Edited by* C. R. Townsend and P. Calow. Sinauer Associates, Inc., Sunderland, Mass. pp. 190–219.

Rock, P., and Williams, O. 1979. Changes in lipid content of the montane vole. Acta Theriol. **24**: 237–247.

Rosenberg, D. K. 1991. Characteristics of northern flying squirrel and Townsend's chipmunk populations in second- and old-growth forests. M.S. thesis, Department of Fisheries and Wildlife, Oregon State University, Corvallis.

Rosenberg, D. K., and Anthony, R. G. 1992. Population characteristics of northern flying squirrels in young second- and old-growth forests in western Oregon. Can. J. Zool. **70**: 161–166.

Witt, J. W. 1991. Fluctuations in the weight and trapping response for *Glaucomys sabrinus* in western Oregon. J. Mammal. **72**: 612–615.