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# Edge Effects and Isolation: Red-Backed Voles Revisited

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**Abstract:** We examined demographic responses of California red-backed voles (*Clethrionomys californicus*) to forest fragmentation in southwestern Oregon at sites where this species has previously shown negative responses to fragmentation. Voles were captured in live traps and released. Voles were rarely caught in clearcuts surrounding 11 forest fragments, but relative vole density did not decrease from the forest-fragment interiors to edges. The first result agrees with previous findings at these sites 6 years earlier, but the latter result does not. There was no evidence that vole response to edge changes with fragment age. Two years of intensive mark-recapture efforts at two forest-fragment sites and two unfragmented (control) sites did not show negative effects of fragmentation on vole survival, an important demographic rate. Vole capture probabilities varied greatly across space and time on these four sites, which may explain the differences in vole responses to edge seen between this and the previous study. These results suggest that reliable appraisal of edge effects may be difficult for many species on small fragments because the data necessary to apply population estimators require great efforts to obtain and the use of indices leads to a confounding of detection probabilities with demographic change.

**Key Words:** abundance, density, edge effects, habitat fragmentation, metareplication, relative density, survival

Efectos de Borde y Aislamiento: *Clethrionomys californicus* Segunda Parte

**Resumen:** Examinamos las respuestas demográficas de ratones (*Clethrionomys californicus*) a la fragmentación de bosques en el suroeste de Oregon en sitios donde esta especie previamente ha mostrado respuestas negativas a la fragmentación. Los ratones fueron capturados y liberados. Raramente capturamos ratones en los claros alrededor de 11 fragmentos de bosque, pero la densidad relativa de ratones no decreció del interior del fragmento de bosque hacia los bordes. El primer resultado, pero no el segundo, coincide con hallazgos previos en estos sitios 6 años antes. No hubo evidencia de la respuesta de ratones a cambios con la edad del fragmento. Dos años de esfuerzos intensivos de marca-recaptura en dos fragmentos de bosque y en dos sitios no fragmentados (control) no mostraron efectos negativos significativos de la fragmentación sobre la supervivencia de ratones, una tasa demográfica importante. Las probabilidades de captura de ratones fueron muy variables en espacio y tiempo en los cuatro sitios, lo que puede explicar las diferencias en las respuestas al borde que encontramos entre el estudio previo y este. Estos resultados sugieren que la valoración confiable de los efectos de borde para muchas especies en fragmentos pequeños puede ser difícil porque se requiere gran esfuerzo para obtener los datos necesarios para aplicar estimadores demográficos y el uso de índices puede confundir probabilidades de detección con cambio demográfico.

**Palabras Clave:** abundancia, densidad, densidad relativa, efectos de borde, fragmentación de hábitat, supervivencia, metareplicación

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## Introduction

A major shortcoming of most empirical studies of habitat fragmentation, and of ecological research in general, is the limited spatial and temporal extent of these projects (Kareiva & Anderson 1988; Weins 1989; Debinski & Holt 2000; Johnson 2002). The use of short-term and geographically limited studies can lead to management recommendations based on underestimates of variability in species responses to fragmentation across time and space, and ultimately may misdirect limited conservation resources. One way to address the problems of short-term studies is to repeat them to determine whether or not observed patterns are consistent over time—an approach termed *metareplication* (Johnson 2002). We report the results of such a study here. We repeated and expanded an earlier study of the effects of edge and isolation on a vole common in old-growth forests of the Pacific Northwest (U.S.A.) to determine whether the negative responses of this species to fragmentation seen in a previous study were consistent over time.

Past studies have provided evidence that the California red-backed vole (*Clethrionomys californicus*) is sensitive to the harvest of old-growth forests (Tevis 1956; Gashwiler 1970). Others suggest that this species serves an ecologically important role as a primary disperser of mycorrhizal fungi (Maser et al. 1978). Indeed, the California red-backed vole and the closely related southern red-backed vole (*C. gapperi*), have served as model species in studies of forest fragmentation and edge effects in the western United States (e.g., Hayward 1999 and references therein). Fieldwork conducted in 1990 and 1991, at the same sites we used in our present study 6 years later, showed that California red-backed voles respond negatively to forest edges and are possibly isolated on patches of old-growth forest surrounded by clearcuts (Mills 1995). Specifically, voles were rarely caught in the clearcuts surrounding forest fragments, the relative density of voles decreased significantly from fragment interiors to edges, and relative density was marginally significantly lower in fragments than control sites.

We repeated this earlier study of edge effects by Mills (1995), using the same field methods and statistical analyses at the same sites, to see whether patterns he found— isolation on forest fragments and decreasing vole density along forest edges—were consistent over time. We also used a more intensive mark-recapture approach at a subset of these sites to determine whether fragmentation effects extend to reduced survival and abundance of adult voles on forest fragments relative to unfragmented control sites. We used these repeated and expanded studies to consider different components of “fragmentation effects” and to determine whether previous results were consistent over time, thus providing important information for land managers seeking to minimize the negative

effects of habitat fragmentation and to speed ecological recovery from these effects.

## Methods

### Site Descriptions and Trapping Protocols

We trapped voles on 11 forest fragments and 2 unfragmented control sites in southwest Oregon (U.S.A.) in the summers of 1997–1999. This part of Oregon has a Mediterranean climate, with wet winters and hot, dry summers. These sites were all unlogged, late-successional forests, with overstories dominated by Douglas-fir (*Pseudotsuga menziesii* Franco) and understories dominated by herbaceous plants. Fragment sites varied in physical characteristics, including size, slope, aspect, and time since adjacent forests were clearcut (Table 1). During each trapping session, each fragment was covered with a grid of Sherman traps spaced at 15-m intervals. Therefore, the trapping effort per area was equivalent across sites, but each site had a different number of traps as a result of differences in fragment sizes. In 1997 and 1998, each of the fragments was also surrounded with four transects of 5–6 traps each. These transects were placed parallel to, and 50 m from, the fragment edge in the surrounding clearcuts.

To examine the effects of fragmentation on vole survival and absolute abundance, we intensively trapped two of the fragment sites (F1 and F2; named E and O in Mills 1995) and two control sites (C1 and C2; near G in Mills 1995), located in continuous forest (>1000 ha in size) near the southern and northern borders of Oregon Caves National Monument, respectively. On the control sites, we used the same grid and peripheral transect configuration used on fragments. Specifically, we set 102 traps in a 17 × 6 grid with 15-m spacing between traps at each site. A transect of 6 traps was set 50 m distant from, and parallel to, each edge of the control trapping grid, thus serving as an analog to the transect in each clearcut of the fragment sites (Tallmon et al. 2003).

We trapped these four sites concurrently from June through August of 1998 and 1999. Our first trapping session at each site was 8 consecutive nights, which allowed us to capture many individuals. All seven subsequent trapping sessions (three more in 1998; four more in 1999) were 4 consecutive nights. Each evening of the trapping sessions, we baited small Sherman live traps with oat groats, sunflower seeds, and approximately 1 cm<sup>3</sup> of fresh apple. We also placed polyester batting inside each trap and placed each trap inside a pint milk container that was lined with batting to increase protection from inclement weather. Each morning we checked and closed all traps to minimize mortality. The four trapping sessions conducted on all sites in the summers of both 1998 and 1999

**Table 1.** Description of forest-fragment and control sites used in study of responses of California red-backed voles (*Clethrionomys californicus*) to habitat fragmentation.<sup>a</sup>

Site	Size (ha)	Distance to forest (m) <sup>b</sup>	Aspect	Slope	Elevation (m)	Year of isolation	Year(s) trapped
<b>Fragment</b>							
F2	3.7	150	W	24	1403	1980	1997–1999
F1	3.0	100	W	32	1342	1987	1997–1999
FB	2.0	120	W	25	671	1973	1997, 1999
W	1.4	60	SE	14	732	1983	1997, 1999
S	1.3	150	E	33	991	1977	1997, 1999
YB	1.3	75	N	35	915	1989	1997, 1999
HD	1.1	110	S	22	976	1965	1997, 1999
Z	1.0	60	S	22	732	1983	1997, 1999
PC	0.9	170	N	35	640	1986	1997, 1999
JT	0.6	50	E	2	991	1988	1997, 1999
F3	0.5	100	W	10	1220	1978	1997–1999
<b>Control</b>							
C1	na	na	SW	12	1580	na	1998, 1999
C2	na	na	W	25	1510	na	1998, 1999

<sup>a</sup>Abbreviation: na, not applicable to control sites.

<sup>b</sup>Distance to the nearest forest more than 7 ha in size.

were separated by 16 days, except the first and second sessions of 1998, which were 20 days apart. This trapping design, referred to as the robust design (Pollock et al. 1990), includes secondary periods (each night of trapping) clustered into primary periods (a trapping session). With this approach, abundances are estimated each primary period based on data from the secondary periods, and apparent survival is estimated for the time intervals between primary periods.

### Edge Effects

We analyzed the vole-trapping data with different approaches at the two spatial scales of our trapping efforts. In our large-scale analysis of edge effects on 11 fragments, we followed the trapping methods and statistical analyses used by Mills (1995) at these sites to allow direct comparisons between studies. The distance from each trap to the nearest forest-clearcut edge was measured, and each trap was assigned to one of four edge classes as a function of distance from the edge: 0–15 m, 16–30 m, 31–45 m, or >45 m. At each site, the number of different animals captured in each edge class over 4 nights of trapping was weighted by the number of traps in that edge class. This can also be interpreted as the number of different animals per trap. At sites for which >1 year of data were collected, these density values for each edge class were averaged across years. We compared the relative densities of voles in each edge class across sites with a one-way analysis of variance that is robust to unequal variances (Rice & Gaines 1989). We also compared the relative densities of voles in the clearcuts to the fragments with a Behrens-Fisher *t* test.

### Survival and Abundance

Data collected from all individuals captured at the two fragments and two control sites that we trapped intensively were analyzed in a robust-design mark-recapture framework with the computer programs RDSURVIV (Kendall et al. 1997) and MARK (White & Burnham 1999). Each individual was assigned to a group according to its sex and the site where it was captured (eight groups). Before analysis was conducted, we developed a set of candidate models with different combinations of temporal, spatial, and sex-specific variation in apparent survival ( $\Phi$ ), capture probability ( $p$ ), and recapture probability ( $c$ ) for the different groups (Appendix). We used RDSURVIV to test for two violations of the assumptions of mark-recapture models: homogeneity in capture probabilities of individuals and independence of individual fates.

Because we did not find evidence of violations of the assumptions of mark-recapture theory under the most complicated (global) model, we compared 15 candidate models in MARK (Appendix). Three additional models (16–18) were added after the original 15 were analyzed to ensure that we had not settled on a bad approximating model. Temporary emigration was set to zero in all models because it was not observed frequently enough to be modeled effectively. Survival estimates are presented for 20-day intervals from the best approximating model as determined with Akaike's information criteria corrected for sample size (AICc).

We focused on adult survival as an appropriate metric to appraise fragmentation effects on vole population dynamics following a sensitivity analysis (Mills & Lindberg 2002). Specifically, a projection matrix model based on *Clethrionomys* vital rates indicated that population

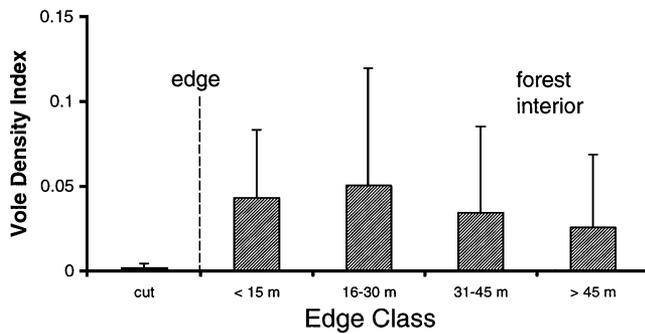


Figure 1. Mean and standard errors of density index for California red-backed voles (*Clethrionomys californicus*) in clearcuts (cut) and forest-fragment edge classes. The distance of traps in each edge class from the nearest forest-clearcut interface are shown on the x-axis.

growth was more affected by changes in adult survival than any other vital rate (Lair 2001).

## Results

We captured 449 individual voles at all sites during the summers of 1997–1999. Of these, only 10 voles were captured in the clearcuts. For the portion of the study that examined edge effects at all 11 fragment sites, we captured 108 voles on the fragments and only 1 vole in the clearcut. The relative density of voles was much lower in clearcuts than in fragments (Fig. 1;  $p = 0.02$ ;  $\bar{x} = 0.0015$  in clearcuts,  $\bar{x} = 0.040$  on fragments). However, our data provide no evidence of a negative edge effect on California red-backed voles on forest fragments. Vole relative density did not decrease from the interior to the edge of forest fragments ( $p = 0.99$ ). Voles were not captured at 3 of the fragment sites (FB, HD, PC), and we detected only one immigration event from a clearcut into a fragment in our entire study.

Estimates of vole survival and abundance in the intensively studied fragments and controls suggest no consistent differences in survival, our best available metric of vole fitness, between voles on control and fragment sites. Survival varied greatly among groups and within groups over time, from 0.18/20 days (SE = 0.097) to 1.00/20 days (SE = 0.000) (Fig. 2). Population sizes in fragment and control sites were small and highly variable, remaining at or below 50 individuals at each site (Table 2). There were deviations from an equal sex ratio both within sites over time and across sites during each trapping session, but neither sex was consistently more common.

There was also large variation in capture and recapture probabilities. The estimates of daily capture probabilities varied from a low of 0.02 (SE = 0.016) at the beginning of the first primary period to a high of 0.82 (SE = 0.032). Re-

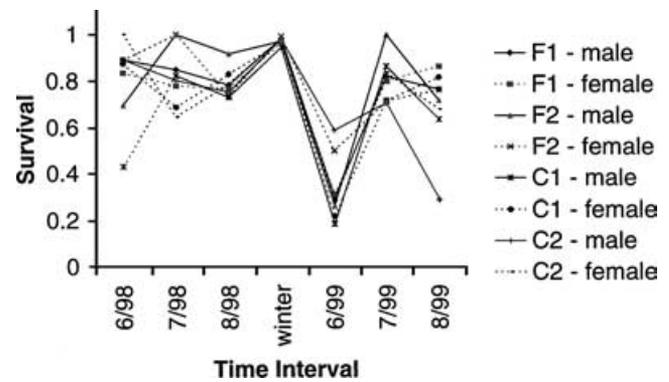


Figure 2. Adult survival estimates for California red-backed voles (*Clethrionomys californicus*) on two forest fragments (F1 and F2) and two contiguous forest control sites (C1 and C2). Each line represents the estimated survival of a group (= a sex at a site) in the best approximating model during each time interval between trapping events. Standard errors are not shown in order to make data presentation easier, but they varied greatly from 0.01 to 0.18.

capture probabilities varied daily across groups from 0.04 (SE = 0.036) to 0.92 (SE = 0.080). Despite this variation, mark-recapture efforts provided precise abundance estimates. The standard errors around the population size estimates for each trapping session were indistinguishable from zero, except for two occasions in 1998 on site C2.

## Discussion

Our finding that voles are much more common in forest fragments than in clearcuts is consistent with the previous results from these sites (Mills 1995) and with previous studies of California red-backed voles in Oregon (Tevis 1956; Gashwiler 1970). However, the finding that the relative density of voles was not lower along forest fragment edges than in fragment interiors conflicts with the work of Mills (1995), who found a negative edge effect at these sites. There are several possible reasons why the edge effect found previously at these sites did not manifest itself. The observed vole edge response may have changed as a result of biotic or abiotic differences over the intervening years between studies. For example, vegetation development in the clearcuts may soften forest edges so that the lack of a negative edge effect in the present study may provide evidence of an ecological recovery in the 6 years between studies. If this were true, then we would expect there still to be a negative edge effect on the fragments most recently affected by timber harvest and less of an effect on the fragments created earlier.

**Table 2.** Estimated number of California red-backed voles (*Clethrionomys californicus*) of each sex (male, female) and total population sizes<sup>a</sup> on forest-fragment sites (F1 and F2) and control sites (C1 and C2) in each of four trapping sessions during the summers of 1998 and 1999.<sup>b</sup>

Fragment Site	1998				1999			
	1	2	3	4	1	2	3	4
F1	21, 17 38	24, 20 44	22, 21 43	20, 17 37	13, 22 35	15, 10 25	6, 16 22	13, 14 27
F2	9, 9 18	9, 13 22	12, 18 30	15, 18 33	20, 16 36	11, 7 18	13, 9 22	7, 12 19
Control								
C1	7, 4 11	10, 14 24	16, 12 28	15, 15 30	9, 17 26	7, 10 17	9, 6 15	5, 7 12
C2	10, 12 22	22, 16 38	28.1, 18 46.1 (0.9)	31.2, 19 50.2 (0.9)	19, 17 36	16, 7 23	12, 7 19	12, 10 22

<sup>a</sup>Population size is given below male and female numbers.

<sup>b</sup>Standard errors are shown in parentheses only where  $>0.01$ .

To investigate the possibility that clearcut regeneration may have led to the lack of a negative edge effect, we used linear regression to conduct an a posteriori analysis of vole relative density at each site on fragment age (time since last clearcut). However, there was no support for a positive effect of fragment age on the relative density of voles on all the fragments (slope =  $-0.002$ ;  $p = 0.18$ ) or on the relative density of voles in the outermost fragment edge class (slope =  $-0.003$ ;  $p = 0.15$ ). In contrast to expectation under the hypothesis of clearcut regeneration leading to an increase in relative vole density, the observed slopes were slightly negative and statistically not significant. This suggests that clearcut regeneration at older fragment sites is not likely to be responsible for the lack of an edge effect in the present study.

Alternatively, the previously observed negative edge effect may not have been observed in the present study because detection (capture) probabilities may have changed over time despite consistent vole responses to edges. Our analysis of the four sites studied intensively with a mark-recapture approach reveals large spatial and temporal variation in capture and recapture probabilities over short time periods. However, because relative density indices confound detection probabilities with density (Nichols & Pollock 1983), we cannot directly address this hypothesis with the existing relative-density data from the 11 fragment sites trapped in both studies.

The numbers of voles captured on the 11 fragment sites on which we examined edge effects ( $n = 108$ ) were similar to the numbers captured in the previous study of these and one additional fragment site ( $n = 135$ ; Mills 1995), but with greater effort in the present study. We did not detect voles at 3 of the 11 sites, one of which did not have voles in the earlier study (HD). However, we detected voles at two sites (Z, YB) where previously none were detected. The capture of few voles in clearcuts in the present and past studies, along with molecular genetic results from

a companion study (Tallmon et al. 2002), suggest that voles are very rare in these clearcuts but may use them frequently for dispersal. Of the 13 voles captured in the clearcuts in 5 years of combined studies of these sites, 9 were males, implying a possible male bias in dispersal (Mills et al. 2003).

Estimates of vole survival and abundance in the intensively studied fragments and controls provided further insight into the effects of habitat fragmentation on voles. There was no evidence that vole survival is generally lower on forest fragments than in large control sites, but survival did fluctuate greatly between the sexes and among sites over time. Despite the variation in survival among groups, there were positive correlations in survival estimates among groups in some of the time intervals, especially in 1999. This may be due to similar responses among groups to weather events in the study area.

California red-backed voles were consistently rare in clearcuts but did not show the negative response to forest fragment edges that was found at these sites 6 years earlier. We did not find any evidence of reduced vole survival on forest fragments relative to control sites, either. Based on these new results, we conclude that voles on forest fragments show fluctuations in population size, adult survival, and detection probabilities over short time intervals. Although demographic and environmental stochasticity may play important roles in vole populations on forest fragments, a companion genetics study provides evidence of much higher rates of immigration into these populations than are implied by the trapping data (Tallmon et al. 2002). This immigration may well ameliorate the potential negative consequences of small, fluctuating population sizes reported here. Our results highlight the limitations of using short-term studies to make management decisions and the importance of metareplication to ensure that biological responses are consistent over time

(Johnson 2002). The unfortunate upshot of these findings is that more effort will be required to resolve the differences in results between the two studies and to make strong inferences about the demographic responses of California red-backed voles to habitat fragmentation.

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## Literature Cited

- Debinski, D. M., and R. D. Holt. 2000. A survey and overview of habitat fragmentation experiments. *Conservation Biology* **14**:342-355.
- Gashwiler, J. S. 1970. Plant and mammal changes on a clear-cut in West-Central Oregon. *Ecology* **51**:1018-1926.
- Hayward, G. D., S. H. Henry, and L. F. Ruggiero. 1999. Response of red-backed voles to recent patch cutting in subalpine forest. *Conservation Biology* **13**:168-176.
- Johnson, D. N. 2002. The importance of replication in wildlife research. *The Journal of Wildlife Management* **66**:919-932.
- Kareiva, P. and M. Anderson. 1988. Spatial aspects of species interactions: the wedding of models and experiments. Pages 38-54 in A. Hastings, editor. *Community ecology*. Springer Verlag, New York.
- Kendall, W. L., J. D. Nichols, and J. E. Hines. 1997. Estimating temporary emigration and breeding proportions using capture-recapture data with Pollock's robust design. *Ecology* **78**:563-578.
- Lair, K. L. 2001. The effects of forest fragmentation and forest edge on southern red-backed vole abundance and survival. M.S. thesis. University of Montana, Missoula.
- Maser, C., J. H. Trappe, and R. A. Nussbaum. 1978. Fungal-small mammal interrelationships with emphasis on Oregon coniferous zones. *Ecology* **59**:799-809.
- Mills, L. S. 1995. Edge effects and isolation: red-backed voles on forest remnants. *Conservation Biology* **9**:395-403.
- Mills, L. S., M. K. Schwartz, D. A. Tallmon, and K. P. Lair. 2003. Measuring and interpreting changes in connectivity for mammals in coniferous forests. Pages 587-613 in C. J. Zabel and R. G. Anthony, editors. *Mammal community dynamics in western coniferous forests: management and conservation issues*. Cambridge University Press, Cambridge, United Kingdom.
- Nichols, J. D., and K. H. Pollock. 1983. Estimation methodology in contemporary small mammal capture-recapture studies. *Journal of Mammalogy* **64**:253-260.
- Pollock, K. H., J. D. Nichols, C. Brownie, and J. E. Hines. 1990. Statistical inference for capture-recapture experiments. *Wildlife Monographs* **107**.
- Rice, W. R., and S. D. Gaines. 1989. One-way analysis of variance with unequal variances. *Proceedings of the National Academy of Sciences of the United States of America* **86**:8183-8184.
- Tallmon, D. A., H. M. Draheim, L. S. Mills, and F. W. Allendorf. 2002. Insights into fragmented vole populations from combined genetic and demographic data. *Molecular Ecology* **11**: 699-709.
- Tallmon, D. A., E. S. Jules, N. Radke, and L. S. Mills. 2003. Of mice and men and trillium: cascading effects of forest fragmentation. *Ecological Applications* **13**:1193-1203.
- Tevis, L. 1956. Responses of small mammal populations to logging of Douglas-fir. *Journal of Mammalogy* **37**:189-196.
- Weins, J. A. 1989. Spatial scaling in ecology. *Function Ecology* **3**:385-397.
- White G. C., and K. P. Burnham. 1999. Program MARK: survival estimation from populations of marked individuals. *Bird Study* **46**(supplement):120-138.

**Appendix. Number of parameters (# P), description, and performance of the candidate models used to examine the effects of forest fragmentation on adult survival and abundance of California red-backed voles (*Clethrionomys californicus*).**\*

No.	Model			Description	# P	$\Delta AICc$
	$\Phi$	p	c			
1	$g^*t$	$g^*t$	$g^*t$	global model: $\Phi, p, c$ vary independently among groups through time	632	350.88
2	$g^*t$	$2^\circ$	$g^*t$	$p$ varies the same way within trap sessions for all groups; $\Phi, c$ vary by group and time	352	200.93
3	$g^*t$	$s^*1^\circ$	$g^*t$	$p$ varies by site and trap session; $\Phi, c$ vary by group and time	376	228.36
4	$g^*t$	$s$	$g^*t$	$p$ site-specific; $\Phi, c$ vary by group and time	348	481.11
5	$g^*t$	$2^\circ$	$g^*t$	$p$ the same among all groups and trap sessions; $\Phi, c$ vary by group and time	345	483.34
6	$g^*t$	$2^\circ$	$2^\circ$	$p, c$ vary the same within all trap sessions for all groups; $\Phi$ varies by group and time	135	162.26
7	$g^*t$	$2^\circ$	$g^*1^\circ$	$c$ varies by group and $1^\circ$ session; $\Phi$ varies by group and time; $p$ varies the same within all trap sessions for all groups	192	0.00
8	$g^*t$	$2^\circ$	$s^*1^\circ$	$c$ unique for each site, each trap session, but constant within each trap session; $p$ varies the same within all trap sessions for all groups; $\Phi$ varies by group and time	160	39.94
9	$g^*t$	$2^\circ$	$s$	$c$ unique at all sites; $p$ varies the same within all trap sessions for all groups; $\Phi$ varies by group and time	132	169.78
10	$g^*t$	$2^\circ$	$g^*1^\circ$	$c$ constant; $p$ varies the same within all trap sessions for all groups; $\Phi$ varies by group and time	129	165.03
11	$g$	$2^\circ$	$g^*1^\circ$	$\Phi$ unique among groups; $p$ varies the same within all trap sessions for all groups; $c$ varies by group and $1^\circ$ session	144	396.51
12	$s$	$2^\circ$	$g^*1^\circ$	$\Phi$ unique among sites; $p$ varies the same within all trap sessions for all groups; $c$ varies by group and $1^\circ$ session	140	390.59
13	control v. fragment	$2^\circ$	$g^*1^\circ$	$\Phi$ different between controls and fragments, constant through time; $p$ varies the same within all trap sessions for all groups; $c$ varies by group and $1^\circ$ session	138	387.90
14	$s^*$ year	$2^\circ$	$g^*1^\circ$	$\Phi$ varies independently among sites each year; $p$ varies the same within all trap sessions for all groups; $c$ varies by group and $1^\circ$ session	144	365.91
15	male v. female	$2^\circ$	$g^*1^\circ$	$\Phi$ varies between males and females, but constant through time; $p$ varies the same within all trap sessions for all groups; $c$ varies by group and $1^\circ$ session	138	390.59
16	$g^*t$	$s^*1^\circ$	$g^*1^\circ$	$\Phi$ varies by group and time; $p$ varies by site and $1^\circ$ session; $c$ varies by group and $1^\circ$ session	210	443.76
17	$g^*t$	$g^*t$	$g^*1^\circ$	$\Phi, p$ vary by group and time; $c$ varies by group and $1^\circ$ session	256	590.34
18	$g^*t$	$2^\circ$	$s^*1^\circ$	$\Phi$ varies by group and time; $p$ varies the same within all trap sessions for all groups; $c$ varies by site and $1^\circ$ session	160	39.92

\*The performance of each model, listed in the order run in program Mark, was evaluated by adjusted Akaike's information criteria (AICc), and  $\Delta AICc = 0.00$  for the top model. Apparent survival ( $\Phi$ ), capture (p), and recapture (c) parameters varied among sites (s), over time (t), between sexes at each site (g), within trapping sessions ( $2^\circ$ ), and among trapping sessions ( $1^\circ$ ).

