

# Small Mammal Responses to Thinning and Wildfire in Ponderosa Pine–Dominated Forests of the Southwestern United States

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## Abstract

As part of a national experiment, the Fire and Fire Surrogate Project, we evaluated the effects of forest thinning on small mammal population densities and total small mammal biomass in ponderosa pine (*Pinus ponderosa*)–dominated forests at 2 study areas in northern Arizona and northern New Mexico, USA. We also evaluated the effects of wildfire on small mammal population densities and biomass after a wildfire burned a portion of one study area. Our statistical methods consisted of estimation of population densities in combined analyses across space and time, followed by a weighted regression analysis of treatment effects on densities. We hypothesized that habitat change postdisturbance would be the critical determinant of population responses to thinning and wildfire within 1 year of disturbances. Our results largely supported this hypothesis, as we documented predicted positive responses to thinning for deer mice (*Peromyscus maniculatus*), gray-collared chipmunks (*Tamias cinereicollis*), and least chipmunks (*T. minimus*). We also observed predicted positive responses to wildfire for deer mice, although our results did not support predicted negative responses to wildfire for least chipmunks. Total small mammal biomass generally increased following both thinning and wildfire. Our results suggest that fuel reduction treatments will have the largest positive impact on small mammal populations in areas where tree densities are especially high. (JOURNAL OF WILDLIFE MANAGEMENT 70(6):1711–1722; 2006)

## Key words

biomass, effective trapping area, fire surrogate, mark–recapture, model selection, *Peromyscus*, population density, small mammals, *Tamias*, thinning, weighted regression, wildfire.

Recently, researchers have focused on investigating changes in fire regimes and stand structure of ponderosa pine (*Pinus ponderosa*)–dominated forests of the southwestern United States (Cooper 1960, Covington and Moore 1994, Moore et al. 1999, Fulé et al. 2001, Allen et al. 2002). These forests apparently experienced frequent fires (2- to 20-yr return interval; Moore et al. 1999) of low to moderate severity in the recent past, resulting in a park-like appearance with mature trees interspersed in forest openings. However, since European settlement of the region, fire suppression, grazing, and logging are thought to have resulted in levels of tree densities and forest fuels outside the historic range of variability, thereby increasing the potential for high-severity wildfires (Cooper 1960, Savage and Swetnam 1990, Covington and Moore 1994, Arno et al. 1995). To reduce this potential, managers are interested in treatments, including mechanical thinning and prescribed fire, to remove excess fuels while moving forests toward historical structural conditions and disturbance intervals (e.g., Covington et al. 1997, Moore et al. 1999, Lynch et al. 2000).

Managers need information that allows better prediction of the effects of fuel reduction treatments to guide management decisions such as type, extent, and location

of treatments. To provide such information, the national Fire and Fire Surrogate (FFS) Project was conceived as a cooperative effort among federal land management agencies, universities, and private organizations. The purpose of the FFS Project was to investigate the relative impacts of fire and fire surrogate treatments (i.e., mechanical thinning) on forest ecology and fire risk in forests throughout the United States that evolved with short-interval, low- to moderate-severity fire regimes (P. Weatherspoon and J. McIver, United States Department of Agriculture Forest Service, unpublished report). The FFS experimental approach applied a similar study design and sampling scheme to 13 study areas across the country, including 2 study areas in ponderosa pine–dominated forests of Arizona and New Mexico, USA. Through the FFS Project, researchers monitored treatment effects on several ecological response variables in the general areas of wildlife, vegetation, fuels and fire behavior, soils, entomology, and pathology.

Compared to forests treated with fuel reduction techniques, untreated forests appear to be at higher risk for severe wildfire (Fulé et al. 2001, Martinson and Omi 2002, Pollet and Omi 2002). Therefore, understanding how effects of fuel reduction treatments differ from the effects of severe wildfires, which may occur more commonly in the absence of fuel reduction treatments, should also help to guide management decisions.

Small mammal population responses to fuel reduction and wildfire may often be of interest to forest managers. Small mammal communities constitute an important component

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of the vertebrate biomass and biodiversity of forests and likely have a substantial role in shaping forest successional patterns through seed consumption and dispersal and hypogeous fungi dispersal (Tevis 1956, Gashwiler 1970, Maser et al. 1978, Price and Jenkins 1986). Small mammals also are primary food sources for predatory species of management concern in southwestern forests, including northern goshawks (*Accipiter gentilis*; Reynolds et al. 1996, Long and Smith 2000) and Mexican spotted owls (*Strix occidentalis lucida*; Ward and Block 1995, Sureda and Morrison 1998, Block et al. 2005).

This work began as an investigation of small mammal responses to thinning treatments in southwestern ponderosa pine-dominated forests, conducted within the FFS Project at the Southwest Plateau study area in northern Arizona and at the Jemez Mountains study area in northern New Mexico. In addition to these treatments, a high-severity wildfire, the Lakes Fire, burned through a portion of the Jemez Mountains study area in 2002 after we had gathered 2 years of small mammal data. This event allowed us the rare opportunity to assess small mammal responses to wildfire through examination of pre- and postfire populations. We evaluated short-term responses (6 months to 1 yr post-disturbance) to forest thinning and wildfire (Converse 2005). We evaluated these responses through changes in population densities of dominant small mammal species and changes in total small mammal community biomass.

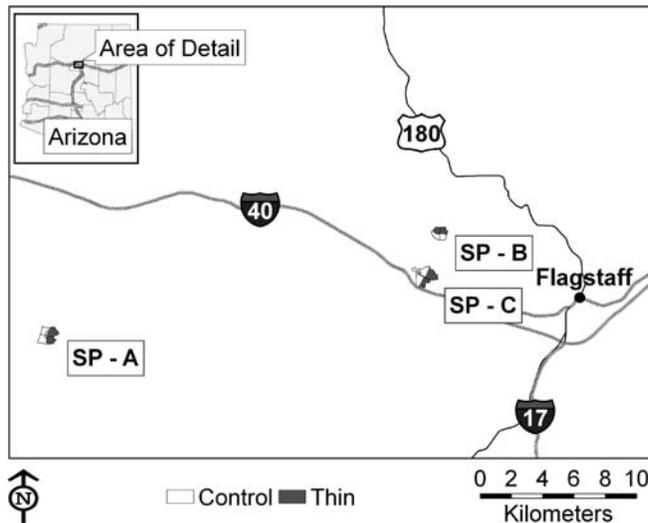
We hypothesized that treatment-induced changes in habitat would determine responses of small mammal densities to treatments. We made predictions of population responses for the dominant small mammal species in our study areas based on habitat associations of the species. The most common species in our study areas, the deer mouse (*Peromyscus maniculatus*), is an omnivorous, early seral-stage generalist known to benefit from disturbances of many kinds (Fitzgerald et al. 1994). We predicted that deer mice would exhibit positive short-term responses to both thinning and fire because of their association with disturbed forest (Tester 1965, Goodwin and Hungerford 1979, Bock and Bock 1983, Kyle and Block 2000). We predicted that chipmunks, including gray-collared chipmunks (*Tamias cinereicollis*) and least chipmunks (*Tamias minimus*), would also exhibit positive short-term responses to thinning. Chipmunks are omnivorous, primarily feeding on herbaceous material and seeds, and are associated with forest openings and with logs and stumps, which are used for feeding, observation, and nesting cover (Hilton and Best 1993, Fitzgerald et al. 1994). We expected that thinning would immediately increase the availability of openings, logs, and stumps, and would also increase food availability through increased herbaceous cover (Bock and Bock 1983, Harris and Covington 1983, Covington et al. 1997, Carey and Wilson 2001, Converse et al. 2006). However, we predicted that chipmunks would decrease following wildfire, due to an expected decline in woody debris (Covington and Sackett 1984, Converse et al. 2006).

## Study Area

The FFS Project national study proposal established the study area design (P. Weatherspoon and J. McIver, unpublished report). The 2 southwestern study areas in the FFS Project were each composed of 3 study sites. Study sites were further divided into 4 experimental units, each assigned to a treatment type (thin, prescribed burn, combination of thin and prescribed burn, control). Study administrators did not assign treatments to the study sites entirely randomly, but sometimes assigned treatments by convenience (e.g., so that thin and combination thin and prescribed burn treatments were next to each other; J. Bailey, Northern Arizona University, personal communication). Because prescribed burning was not completed on the southwestern study areas within the time frame of this research, only the thinning portion of the FFS Project study design is examined here; we treated combination thin and prescribed burn units as thin units and we treated prescribed burn units as control units in our analyses. All sampling within the experimental units was keyed to a permanent grid system of 36 points placed 50 m apart, generally in a 6 × 6 array but sometimes in an oblong or nonrectangular array. The total area of each sampling grid was approximately 6.25 ha. Fifty-meter buffers surrounded each of the sampling grids (i.e., total area of the treated areas was approx. 12.25 ha).

The Southwest Plateau study area (SPSA; Fig. 1) was located on the Coconino and Kaibab national forests west of Flagstaff, Arizona, USA, between 2,100 m and 2,300 m elevation. It was composed of one study site, Southwest Plateau-A (SP-A), located on the Kaibab National Forest (35°N, 112°W), and 2 study sites, Southwest Plateau-B (SP-B) and Southwest Plateau-C (SP-C), located on the Coconino National Forest (35°N, 111°W). At all 3 SPSA study sites, experimental units were arranged in a 2 × 2 square block, with experimental units adjacent within the blocks. Ponderosa pine was the sole tree species throughout the 3 study sites, with the exception of a few (<20% of basal area; J. Bailey, unpublished data) Gambel oak (*Quercus gambelii*) and alligator juniper (*Juniperus deppeana*) at SP-A. Common understory plants included (J. Bailey, unpublished data) yarrow (*Achillea millefolium*), pine dropseed (*Blepharoneuron tricholepis*), sedges (*Carex* spp.), and squirreltail (*Sitanion hystrix*), though drought conditions in the southwestern United States at the time of the study likely resulted in relatively low herbaceous cover. The SP-A site had a few low rocky ridges, but otherwise the sites lacked substantial topographic relief. All of the SPSA study sites had been precommercial thinned during the previous 30 years, with ≥2 prior entries of thinning.

The Jemez Mountains study area (JMSA; Fig. 2) was located on the Santa Fe National Forest, northwest of Jemez Springs, New Mexico, USA (35°N, 106°W), at elevations ranging from 2,400 m to 2,600 m. Here we present data gathered at 2 study sites, Jemez Mountains-B (JM-B) and Jemez Mountains-C (JM-C). We have not included data from a third study site because no treatments were



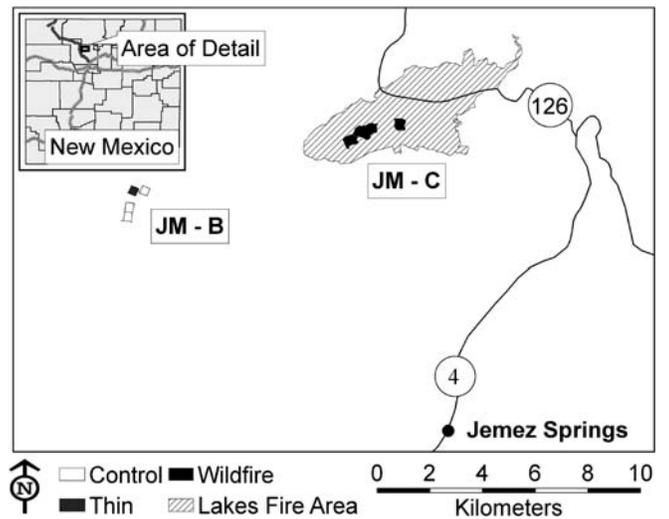
**Figure 1.** The Southwest Plateau study area (SPSA) of the Fire and Fire Surrogate Project, depicting the location of 3 study sites in northern Arizona, USA, each of which had 2 thinned experimental units and 2 controls. We trapped small mammal species on the experimental units in 2000–2002 (pretreatment) and 2003 (posttreatment).

completed there during the period over which we gathered data. At the JM-B site, 2 adjacent experimental units were <1 km from the 2 other adjacent experimental units. At the JM-C site, the experimental units were arranged in a string along the northern edge of a mesa top. Ponderosa pine dominated both the JM-B and JM-C study sites, with southwestern white pine (*Pinus strobiformis*), Douglas-fir (*Pseudotsuga menziesii*), Gambel oak, and aspen (*Populus tremuloides*) present in lesser amounts. Common understory shrubs (J. Bailey, unpublished data) included Woods rose (*Rosa woodsii*), kinnikinnick (*Arctostaphylos uva-ursi*), and Oregon grape (*Berberis aquifolium*). Common herbaceous plants included yarrow, sedges, muttongrass (*Poa fendleriana*), and squirreltail. Both the JM-B and JM-C sites included hills and rocky ridges. Information on management history was not available for the study sites, but the stands had undergone logging in the past.

## Methods

### Small Mammal Trapping

We conducted small mammal trapping annually from 2000 to 2003 at the SPSA and from 2001 to 2003 at the JMSA. Animal care protocols were approved by the Colorado State University Animal Care and Use Committee, and trapping was conducted under permits from the states of New Mexico and Arizona. Trapping occurred in July and August each year during 2 consecutive 5-day sessions at each study area. We trapped half the experimental units at each study site, randomly assigned, in the first session, and we trapped the other half in the second session. We used 2 different densities of traps; after we conducted a pilot study on 2 experimental units at the SPSA study site in 2001, we increased trapping density from large ( $7.6 \times 8.9 \times 22.9$  cm) Sherman live-traps (H. B. Sherman Traps, Tallahassee, Florida) every 50 m and extra-large ( $10.2 \times 11.4 \times 38.1$  cm)



**Figure 2.** The Jemez Mountain study area (JMSA) of the Fire and Fire Surrogate Project, depicting the location of 2 study sites in northern New Mexico, USA. Study site B (JM-B) had one thinned experimental unit and 3 controls. Study site C (JM-C) experienced a wildfire throughout its 4 experimental units. The map also shows the area affected by the Lakes Fire in Aug 2002. We trapped small mammal species on the experimental units in 2001–2002 (pretreatment) and 2003 (posttreatment and postwildfire).

Sherman live-traps every 100 m, to large Sherman live-traps every 25 m and extra-large Sherman live-traps every 50 m (increased trap density applied at 2 experimental units in 2001 and everywhere in 2002 and 2003). We increased trapping density to increase capture probabilities, and hence increase precision of abundance estimates (Converse et al. 2004). We modeled the difference in trap density as an effect on capture probability (described below).

We positioned traps along small mammal trails, at the openings of burrow holes, or in proximity to downed woody debris. We used a wood shingle to shade and insulate traps. We placed polyester filling at the back of each trap for additional insulation, along with approximately 20 mL of a bait mixture of rolled oats and chicken feed. We also trailed a small amount of bait into the entrance of each trap. We checked traps during both morning and afternoon to yield 10 trapping occasions on each unit each year. During trapping, we recorded the following data for each animal: trap location and trap size, species, new or recapture, individual identity, age class, sex, mass, reproductive condition, and release condition. We individually identified animals with 2 unique ear tags.

### Thinning Treatments and Wildfire

Thinning treatments were designed by study administrators and carried out by thinning contractors so as to simultaneously retain the largest trees and create clumps of trees separated by larger, semi-open spaces. Researchers report that this more closely simulates historical conditions in southwestern ponderosa pine forests (Covington et al. 1997). On the SPSA, 2 experimental units at both the SP-B and SP-C sites were thinned during the fall of 2002, with piling of slash completed in the spring of 2003.

Thinning began on 2 experimental units at the SP-A site in the fall of 2002 but was not completed until the spring of 2003. At the SP-A site, trees were felled primarily with a feller-buncher (a machine that strips branches from and cuts trees) and slash was piled. At the SP-B and SP-C sites, trees were hand-felled and slash was piled; slash piles were slightly smaller and more numerous at the SP-B and SP-C sites than at the SP-A site. Slash was left after the treatments and was still present in the experimental units during small mammal trapping in 2003. At the JMSA, one experimental unit at the JM-B site was thinned in the spring of 2003. Though some piles existed, slash was generally not piled but was left scattered on the ground and was still in the unit during the trapping season of 2003. Thinning was not completed at the remaining experimental unit slated for thinning at the JM-B site because of logistical difficulties. Disturbance of the soil after thinning appeared to be more severe at the JMSA than at the SPSA, presumably due to the thinning methods used and the greater topographic relief at the JMSA.

The Lakes Fire (approx. 1,700 ha) burned through the entire JM-C site at the JMSA in late August 2002. Tree mortality was nearly complete throughout the majority of the 4 experimental units. The fire consumed needles and small branches on a majority of the trees and almost completely consumed ground cover, leaving bare soil throughout the site, except in some small clearings. The United States Forest Service treated the burned slope to the north of the JM-C site with aerial seeding on 11–12 October 2002, with the goal of reducing postfire erosion. The treatment involved application of grass seed, including mountain brome (*Bromus marginatus*; 30% of mix), slender wheatgrass (*Elymus trachycaulus*; 30%), annual rye grass (*Lolium multiflorum*; 30%), and barley (*Hordeum vulgare*; 10%), at a nominal density of approximately 25 kg/ha. Although the seed was not intended for the JM-C experimental units, it was apparent that some seed had blown into the north portion of the experimental units because of the presence of seeded grasses in June 2004.

### Data Analysis

The analysis of responses to thinning and wildfire occurred in 4 steps. First, we estimated abundances for each species each year in each experimental unit, based on the mark-recapture data. Second, we estimated effective trapping area for each species each year in each unit through models of mean maximum distance moved. Third, we calculated species-specific densities, total small mammal biomass, and variance-covariance matrices for densities and biomass in each unit each year. Finally, we conducted weighted least-squares regression analyses to examine the effects of habitat disturbances (i.e., thinning and wildfire) on densities of the most common small mammal species at each study area and on total small mammal biomass at each study area. Throughout the analysis, we employed an information-theoretic philosophy of model selection and multi-model inference (Burnham and Anderson 2002). We based model selection on Akaike's Information Criterion (AIC; Akaike

1973) with a small sample correction (AIC<sub>c</sub>; Hurvich and Tsai 1989), and we based model averaging on Akaike weights, which can be treated as a weight of evidence in favor of a particular model. At each step in the analysis, we specified statistical model sets a priori, to strengthen inference and lessen the risk of identifying spurious effects (Anderson et al. 2001).

**Abundance.**—We estimated abundance for each unit in each year with the conditional likelihood closed capture–recapture model of Huggins (1989, 1991). The conditional likelihood model estimates capture probabilities based on animal encounter histories and can account for heterogeneity in capture probabilities due to temporal effects, behavioral responses to capture, and individual heterogeneity (Model M<sub>tbl</sub>; Otis et al. 1978). The model generates estimates of abundance based on the estimated capture probabilities and the number of individuals captured. We conducted abundance estimation in Program MARK 3.2 (White and Burnham 1999). We treated experimental units in each year of the study as groups in the analysis, and thus we obtained abundance estimates for each unit in each year (i.e., we combined data across experimental units and years to obtain abundance estimates for each experimental unit in each year and we used auxiliary variables to model differences in detection probabilities across experimental units and years; e.g., Bowden et al. 2003). This approach is useful because of its increased statistical efficiency (i.e., reduced variances of estimates) compared to estimating abundance separately in each experimental unit and year combination.

We used age as an individual covariate to account for heterogeneity in capture rates. We classified animals as either adults or subadults based primarily on mass and secondarily on external evidence of reproductive status if there was uncertainty in mass measurements (McCrary and Rose 1992). We defined deer mice and brush mice (*Peromyscus boylii*) as adult when  $\geq 14$  g, long-tailed voles (*Microtus longicaudus*) when  $\geq 30$  g, least chipmunks when  $\geq 35$  g, gray-collared chipmunks and cliff chipmunks (*Tamias dorsalis*) when  $\geq 50$  g, Mexican woodrats (*Neotoma mexicana*) when  $\geq 100$  g, and golden-mantled ground squirrels (*Spermophilus lateralis*) when  $\geq 150$  g.

We proposed multiple a priori models to estimate capture probabilities. We included a time of day effect (morning vs. evening trap check) and a behavioral response to capture in all models because observations during data collection indicated that these were clearly important factors. At both study areas, we included age of individual, either year or session within year, and either experimental unit or site as effects in the models. For the SPSA analyses, we also included trap density (increased density at 2 experimental units in 2001 and at all units in 2002 and 2003) and treatment (thinning). For the JMSA analysis, we also included treatment (thinning or wildfire), but we did not consider trap density in the JMSA analysis because trap density was completely confounded with year. We included all possible combinations of the effects for 72 total abundance estimation models in both the SPSA and JMSA

analyses. We averaged the resulting abundance estimates and variance–covariance matrices across models based on Akaike weights to account for model selection uncertainty (Burnham and Anderson 2002, 2004).

**Effective trapping area.**—Estimation of abundance via mark–recapture methods from a trapping grid results in an estimate that pertains to an unknown total area because animals whose home ranges are partially outside the trapping grid may be captured on the trapping grid, resulting in an effective trapping area that is larger than the grid itself. Therefore, we used the mean maximum distance moved (MMDM) method to estimate the effective trapping area to which abundance estimates applied (Wilson and Anderson 1985).

We calculated the maximum distance moved (m) between any 2 traps for each marked animal with  $\geq 2$  captures in an experimental unit in 1 year. As for the abundance estimation, we combined data across experimental units and years to facilitate efficient estimation of MMDM. We then specified multiple analysis of variance models to estimate MMDM (PROC GLM; SAS Institute 2003). For the analyses at both study areas, we proposed candidate models with MMDM varying by year, unit, site, or a constant model. For the SPSA analysis, we additionally considered models with MMDM varying by treatment (thinning) and trap density. For the JMSA analysis, we also considered models with MMDM varying by treatment (thinning or wildfire). Thus, we examined 6 models in the analyses at each study area. We only considered single-variable models and a smaller model set, as compared to the abundance estimation procedure, because less information is available in the capture–recapture data on movement than on capture probability. For each model, we then added a buffer strip, with a width of one-half the estimated MMDM (MMDM is limited to values  $\geq 0$ ), to the area of each trapping grid to estimate the effective trapping area (Otis et al. 1978, Wilson and Anderson 1985). Finally, we averaged the resulting effective trapping area estimates and variance–covariance matrices across models based on Akaike weights to account for model selection uncertainty (Burnham and Anderson 2002, 2004).

**Densities, biomass, and variance–covariance matrices.**—We calculated species-specific densities in each experimental unit each year as the abundance divided by the effective trapping area. For the analysis of total biomass, we used the minimum adult mass in grams (described above) as a multiplier to convert density estimates to biomass estimates, and then we summed the total estimated mass over all marked species at each study area. Variance–covariance matrices of the density estimates and total biomass estimates were necessary for the weighted regression analysis. We computed these matrices by delta method transformations of the model-averaged variance–covariance matrices of the abundance estimates and the model-averaged variance–covariance matrices of effective trapping area (Seber 1982).

Weighted analysis cannot be conducted with variances of

zero because the variance–covariance matrix is singular. Variances of zero occurred in the abundance variance–covariance matrix for a species when no animals of that species were caught on a given experimental unit in a given year. In order to provide positive variances in these cases, we fit a linear regression (PROC REG; SAS Institute 2003) of the natural log of positive variances against their corresponding density estimates and determined the regression intercept (Franklin 1997). The exponential of the regression intercept then served as the variance for the zero density estimates. We used this method for the most common species at each study area, which we analyzed singly, as well as for the less common species before we included them in the analysis of total biomass. The only exception was the long-tailed vole, which we only caught on one experimental unit in 1 year, thus making a regression impossible.

**Treatment effects.**—We conducted the analysis of treatment effects with weighted least-squares regression (Draper and Smith 1998). A traditional (i.e., unweighted) regression analysis was inappropriate because of the nonzero sampling covariances between the density estimates, which we induced through the abundance and effective trapping area estimation procedures, wherein we combined data across experimental units and years for efficient estimation.

We specified multiple a priori models describing predicted responses of densities to treatments. We used site, year, and treatments as factors in the models. In the SPSA data analysis, we treated thinning as 3 factors by nesting thinning within the 3 study sites. We treated thinning in this way because important interaction effects were evident after an initial set of analyses. In the JMSA analysis, there were 2 treatments, thinning and wildfire, and we did not consider nested effects because treatments were naturally nested within sites. We ran all combinations of the variables, for 8 models in the SPSA analysis and 16 models in the JMSA analysis.

Draper and Smith (1998) describe computation of a vector of effect sizes ( $\hat{\beta}_i$ ) and an associated variance–covariance matrix ( $\hat{\Sigma}_i$ ) for weighted regression analysis. We describe computation of  $AIC_c$  (Akaike 1973, Hurvich and Tsai 1989) for model selection in a weighted regression framework in Appendix A. Based on the computed  $AIC_c$  for each model, we employed information-theoretic model selection and multi-model inferential methods (Burnham and Anderson 2002). These included Akaike weights (which we computed based on each model's relative  $AIC_c$  value ( $\Delta AIC_c$ ) and treated as a weight of evidence in favor of a particular model), model-averaged effect sizes and 95% confidence intervals, and relative importance values for variables, calculated by summing the Akaike weights across all models in which a given variable appears (Burnham and Anderson 2002). Recent work has indicated that a relative importance value, of  $\geq 0.40$  based on Akaike weights, suggests that a variable is related to the process of interest (G. C. White, Colorado State University, unpublished data). We used each of these multiple lines of evidence from which to make inference about the results of our analyses.

**Table 1.** Model selection results<sup>a</sup> from weighted regression analysis of treatment effects on deer mouse densities at the Southwest Plateau study area, northern Arizona, USA, 2000–2003.

Model	AIC <sub>c</sub>	ΔAIC <sub>c</sub>	w <sub>i</sub>	K
Density{site(thin) <sup>b</sup> }	8.294	0.000	0.65	5
Density{constant}	11.038	2.745	0.17	2
Density{site + site(thin)}	12.315	4.021	0.09	7
Density{site}	12.989	4.696	0.06	4

<sup>a</sup> Results include Akaike's Information Criterion corrected for small sample size (AIC<sub>c</sub>), relative AIC<sub>c</sub> (ΔAIC<sub>c</sub>), Akaike weight (w<sub>i</sub>), and number of parameters (K) for models with ≥5% of the w<sub>i</sub>.

<sup>b</sup> The thinning effect was nested within study sites.

## Results

We caught 2 species most commonly at each study area, with all other species contributing <25 total individuals per study area. At the SPSA, deer mice ( $n = 486$  marked individuals) and gray-collared chipmunks ( $n = 304$ ) were the dominant species. Estimated deer mouse densities ranged from zero (SE = 0) to 8.5 (SE = 1.6) individuals per hectare, and gray-collared chipmunk densities ranged from zero (SE = 0) to 3.3 (SE = 0.4) individuals per hectare. Total small mammal biomass at the SPSA also included golden-mantled ground squirrels ( $n = 21$ ), Mexican woodrats ( $n = 19$ ), and cliff chipmunks ( $n = 11$ ). At the JMSA, deer mice ( $n = 559$ ) and least chipmunks ( $n = 153$ ) were the dominant species. Estimated deer mouse densities ranged from 0.4 (SE = 0.2) to 9.6 (SE = 0.9) individuals per hectare, and least chipmunk densities ranged from 0 (SE = 0) to 1.9 (SE = 0.7) individuals per hectare. Total small mammal biomass also included long-tailed voles ( $n = 23$ ), Mexican woodrats ( $n = 21$ ), and golden-mantled ground squirrels ( $n = 12$ ). Small mammal community composition appeared to be generally stable before and after treatments, with the exception of long-tailed voles, which we only captured in 2003 (i.e., after thinning) on the thinned experimental unit at the JMSA. At both study areas, *Peromyscus* spp. captures included small numbers of brush mice ( $n = 2$  at SPSA,  $n = 5$  at JMSA) in addition to deer mice, but we combined these individuals with deer mice before we conducted the analyses because numbers were low; we refer to all *Peromyscus* spp. as deer mice throughout this paper.

There existed evidence that capture probabilities and MMDM varied by many of the modeled factors, including thinning and wildfire (i.e., thinning and wildfire impacted the behavior of animals). Top-ranked models of capture probabilities included a thinning effect for gray-collared chipmunks at the SPSA and for least chipmunks at the JMSA, and a wildfire effect appeared in the top-ranked capture probabilities model for deer mice at the JMSA (Converse 2005). Based on results from these top models, thinning had a positive impact on capture probabilities of both gray-collared chipmunks (effect size = 1.23, SE = 0.47) and least chipmunks (effect size = 1.56, SE = 0.33), whereas wildfire had a negative impact on capture probabilities of deer mice (effect size = -0.86, SE = 0.20), where effect sizes are on a logit scale. The top model of mean maximum

**Table 2.** Model-averaged effect sizes, 95% confidence intervals, and relative importance values<sup>a</sup> from weighted regression analysis of treatment effects on deer mouse densities at 3 study sites (SP-A, SP-B, and SP-C) at the Southwest Plateau study area, northern Arizona, USA, 2000–2003.

Variable	Effect size	95% CI	Relative importance value
Site <sup>b</sup>			0.15
Yr			0.03
Thin at SP-A	0.24	-0.22, 0.70	0.76 <sup>c</sup>
Thin at SP-B	-0.17	-0.45, 0.11	0.76
Thin at SP-C	1.11	-0.57, 2.79	0.76

<sup>a</sup> Calculated by summing the Akaike weights across all models in which the variable appears.

<sup>b</sup> Site and year effect estimates are blocking effects specific to sites and years, and we do not report them here for the sake of brevity.

<sup>c</sup> Relative importance values are the same for all levels of the thin effect because we always grouped these effects together in models.

distance moved by gray-collared chipmunks at the SPSA included a thinning effect in which MMDM was larger in thinned than in control experimental units (control MMDM = 96.30 m, SE = 4.41; thinned MMDM = 122.62 m, SE = 12.74).

Regarding the response of population densities, the analysis supported predicted positive responses of deer mice to thinning everywhere except the SP-B study site on the SPSA. The top-ranked weighted regression model included only the thin effect (which was nested within site); this model had an Akaike weight of 0.65 (Table 1). The thin effect had a high relative importance value (0.76; i.e., thinning was associated with models that carried 76% of the total weight [Table 2]). The thinning effect was positive at both the SP-A and SP-C sites, but the effect was negative at the SP-B site, although in all cases the 95% confidence intervals on the model-averaged estimates included zero. At the JMSA, the top-ranked model for deer mice included year, thinning, and wildfire effects, and had an Akaike weight of 0.59 (Table 3). The relative importance value of the positive thinning effect was 0.89, and the 95% confidence interval did not include zero (Table 4).

Deer mouse densities also exhibited predicted positive responses to wildfire. At the JMSA, as noted above, the top-ranked regression model for deer mice included year, thinning, and wildfire effects (Table 3). The relative importance value of the positive wildfire effect was 0.77, with a 95% confidence interval that only marginally included zero (Table 4).

The analysis also largely supported predicted positive responses of gray-collared and least chipmunk densities to thinning. At the SPSA, only one model of gray-collared chipmunks had nearly all of the Akaike weight (0.95) for the model set. This model included both the site effect and the thin effect (which was nested within site). The relative importance value of thinning was high (1.00; Table 5). We captured few gray-collared chipmunks at the SP-A study site, and the estimate of the thinning effect there was nearly zero. Elsewhere, exhibiting a similar pattern as for the deer

**Table 3.** Model selection results<sup>a</sup> from weighted regression analysis of treatment effects on deer mouse densities at the Jemez Mountains study area, northern New Mexico, USA, 2001–2003.

Model	AIC <sub>c</sub>	ΔAIC <sub>c</sub>	w <sub>i</sub>	K
Density{year + thin + fire}	46.499	0.000	0.59	6
Density{site + year + thin + fire}	49.555	3.056	0.13	7
Density{site + year + thin}	50.310	3.811	0.09	6
Density{year + thin}	50.359	3.860	0.09	5

<sup>a</sup> Results include Akaike's Information Criterion corrected for small sample size (AIC<sub>c</sub>), relative AIC<sub>c</sub> (ΔAIC<sub>c</sub>), Akaike weight (w<sub>i</sub>), and number of parameters (K) for models with ≥5% of the w<sub>i</sub>.

mouse analysis, the estimate of the thinning effect at the SP-C site was positive, while the estimate at the SP-B site was negative, though only at the SP-C site did the 95% confidence interval exclude zero. For least chipmunks at the JMSA, the top-ranked model had an Akaike weight of 0.47 and included site and thinning effects (Table 6). The relative importance value of the positive thinning effect was 0.96 and the 95% confidence interval did not include zero (Table 7).

The analysis did not support the predicted negative response of least chipmunk densities to wildfire. The top-ranked model for least chipmunks at the JMSA did not include a wildfire effect (Table 6), the relative importance value of the wildfire effect was 0.19, and the effect estimate was nearly zero (Table 7).

Total biomass generally increased due to thinning at the SPSA, where the top model included site and thinning (nested within site) effects (Table 8) and had an Akaike weight of 0.73. The relative importance value of thinning (0.92) was high, and the effect was positive at the SP-A and SP-C study sites and negative at the SP-B site, but only the SP-C estimate had a 95% confidence interval that did not include zero (Table 9). At the JMSA, the top-ranked biomass model included a wildfire effect, with an Akaike weight of 0.28 (Table 10). The top-ranked model including a thinning effect had an Akaike weight of 0.11. The estimated effect of the wildfire was positive and the relative importance value was 0.56; the relative importance value for the positive thinning effect was a low 0.23 (Table 11). In both cases the 95% confidence intervals included zero.

**Table 4.** Model-averaged effect sizes, 95% confidence intervals, and relative importance values<sup>a</sup> from weighted regression analysis of treatment effects on deer mouse densities at the Jemez Mountains study area, northern New Mexico, USA, 2001–2003.

Variable	Effect size	95% CI	Relative importance value
Site <sup>b</sup>			0.25
Yr			1.00
Thin	3.36	0.06, 6.66	0.89
Fire	1.78	−0.75, 4.31	0.77

<sup>a</sup> Calculated by summing the Akaike weights across all models in which the variable appears.

<sup>b</sup> Site and year effect estimates are blocking effects specific to sites and years, and we do not report them here for the sake of brevity.

**Table 5.** Model-averaged effect sizes, 95% confidence intervals, and relative importance values<sup>a</sup> from weighted regression analysis of treatment effects on gray-collared chipmunk densities at 3 study sites (SP-A, SP-B, and SP-C) at the Southwest Plateau study area, northern Arizona, USA, 2000–2003.

Variable	Effect size	95% CI	Relative importance value
Site <sup>b</sup>			0.98
Yr			0.03
Thin at SP-A	−0.01	−0.29, 0.26	1.00 <sup>c</sup>
Thin at SP-B	−0.18	−0.39, 0.04	1.00
Thin at SP-C	0.97	0.50, 1.43	1.00

<sup>a</sup> Calculated by summing the Akaike weights across all models in which the variable appears.

<sup>b</sup> Site and year effect estimates are blocking effects specific to sites and years, and we do not report them here for the sake of brevity.

<sup>c</sup> Relative importance values are the same for all levels of the thin effect because we always grouped these effects together in models.

## Discussion

We found that we could predict with some accuracy responses of common small mammal species to fuel reduction treatments and wildfire based on habitat associations. We documented, as predicted, generally positive responses by deer mice to both thinning and wildfire and generally positive responses by chipmunk species to thinning. However, we did not find strong evidence for predicted negative responses by chipmunks to wildfire.

Despite the overall accuracy of our predictions of positive thinning responses, there were inconsistencies in these responses at the SPSA, which may be illuminated by a comparison of the SP-B and SP-C sites. The SP-B site showed estimated responses to thinning by deer mice and chipmunks that were slightly negative, while the nearby SP-C site, which had a similar small mammal community, showed strong positive responses to thinning by deer mice and chipmunks. Comparisons of pretreatment data on tree basal area and tree density at the SP-B and SP-C sites (J. Bailey, unpublished data) indicate that while average tree basal area was similar at the 2 sites pretreatment, average tree density was greater at the SP-C site, where tree densities ranged from 611–906 trees/ha (mean = 798 trees/ha), compared to 387–701 trees/ha (mean = 540 trees/ha) at the SP-B site. Therefore, the trees at the SP-C site were on

**Table 6.** Model selection results<sup>a</sup> from weighted regression analysis of treatment effects on least chipmunk densities at the Jemez Mountains study area, northern New Mexico, USA, 2001–2003.

Model	AIC <sub>c</sub>	ΔAIC <sub>c</sub>	w <sub>i</sub>	K
Density{site + thin}	65.895	0.000	0.47	4
Density{thin}	67.988	2.093	0.17	3
Density{site + thin + fire}	69.110	3.214	0.09	5
Density{year + thin}	69.225	3.329	0.09	5
Density{thin + fire}	69.878	3.983	0.06	4
Density{site + year + thin}	70.286	4.391	0.05	6

<sup>a</sup> Results include Akaike's Information Criterion corrected for small sample size (AIC<sub>c</sub>), relative AIC<sub>c</sub> (ΔAIC<sub>c</sub>), Akaike weight (w<sub>i</sub>), and number of parameters (K) for models with ≥5% of the w<sub>i</sub>.

**Table 7.** Model-averaged effect sizes, 95% confidence intervals, and relative importance values<sup>a</sup> from weighted regression analysis of treatment effects on least chipmunk densities at the Jemez Mountains study area, northern New Mexico, USA, 2001–2003.

Variable	Effect size	95% CI	Relative importance value
Site <sup>b</sup>			0.65
Yr			0.17
Thin	1.32	0.38, 2.25	0.96
Fire	−0.02	−0.17, 0.13	0.19

<sup>a</sup> Calculated by summing the Akaike weights across all models in which the variable appears.

<sup>b</sup> Site and year effect estimates are blocking effects specific to sites and years, and we do not report them here for the sake of brevity.

average smaller and more numerous. Stands of this type, with small, closely spaced trees, appear to limit populations of deer mice and chipmunks (Hamilton and Cook 1940) and, based on our results, thinning of such stands may result in the greatest short-term response in populations of these species. This result highlights the importance of pre-disturbance conditions in determining responses to thinning and wildfire. If habitat is poor for small mammals before disturbance, it is more likely to improve after disturbance. The thinned experimental unit at the JM-B site, where we observed strong positive responses by both deer mice and least chipmunks, also had stands that were thick with small trees and had few openings prior to treatment.

Previously, researchers have suggested positive responses to thinning by deer mice (Wilson and Carey 2000, Carey and Wilson 2001, Suzuki and Hayes 2003). Immediate increases in deer mouse populations after thinning may be due to increases in invertebrate food sources (Ahlgren 1966), herbaceous food and cover (Wilson and Carey 2000), conifer seed in slash piles, and coarse woody debris cover (Carey and Johnson 1995, Suzuki and Hayes 2003, but see Hadley and Wilson 2004, Manning and Edge 2004, and Block et al. 2005). Indeed, the presence of slash after thinning, whether piled (at the SPSA) or scattered (at the JMSA), appeared to provide focal points for deer mouse activity in our study.

Researchers have also documented positive responses of deer mice to prescribed fire and wildfire, including severe wildfire (Tester 1965, Ahlgren 1966, Krefting and Ahlgren 1974, Bock and Bock 1983, Martell 1984, Kyle and Block

**Table 8.** Model selection results<sup>a</sup> from weighted regression analysis of treatment effects on total small mammal biomass at the Southwest Plateau study area, northern Arizona, USA, 2000–2003.

Model	AIC <sub>c</sub>	ΔAIC <sub>c</sub>	w <sub>i</sub>	K
Biomass{site + site(thin) <sup>b</sup> }	8.978	0.000	0.73	7
Biomass{site + year + site(thin)}	11.650	2.672	0.19	10
Biomass{site}	13.621	4.644	0.07	4

<sup>a</sup> Results include Akaike's Information Criterion corrected for small sample size (AIC<sub>c</sub>), relative AIC<sub>c</sub> (ΔAIC<sub>c</sub>), Akaike weight (w<sub>i</sub>), and number of parameters (K) for models with ≥5% of the w<sub>i</sub>.

<sup>b</sup> The thinning effect was nested within study sites.

**Table 9.** Model-averaged effect sizes, 95% confidence intervals, and relative importance values<sup>a</sup> from weighted regression analysis of treatment effects on total small mammal biomass at 3 study sites (SP-A, SP-B, and SP-C) at the Southwest Plateau study area, northern Arizona, USA, 2000–2003.

Variable	Effect size	95% CI	Relative importance value
Site <sup>b</sup>			1.00
Yr			0.20
Thin at SP-A	6.52	−40.35, 53.39	0.92 <sup>c</sup>
Thin at SP-B	−42.31	−105.22, 20.60	0.92
Thin at SP-C	70.06	9.52, 130.60	0.92

<sup>a</sup> Calculated by summing the Akaike weights across all models in which the variable appears.

<sup>b</sup> Site and year effect estimates are blocking effects specific to sites and years, and we do not report them here for the sake of brevity.

<sup>c</sup> Relative importance values are the same for all levels of the thin effect because we always grouped these effects together in models.

2000). These responses may be related to increased food sources, such as forbs, even with severe wildfire (Kyle and Block 2000). The availability of food sources may have increased after the severe wildfire in this study if a reduction in the litter layer exposed forb or pine seeds in the soil or, if some pine seeds survived the fire in the canopy, dispersed during the fall after the fire and were more easily located by mice during the fall or following spring. In addition, some small unburned or lightly burned patches in the area of the fire may have allowed for easy foraging by deer mice. However, the possibility exists that the positive response of deer mice was due partly to the grass seeding operation carried out in October of 2002, in which an unknown amount of grass seed apparently drifted into the experimental units. While the amount of coarse woody debris likely decreased after the wildfire (Covington and Sackett 1984, Arno et al. 1995, Converse et al. 2006), and given some evidence of a positive relationship between deer mouse abundance and coarse woody debris (Goodwin and Hungerford 1979, Graves et al. 1988, Carey and Johnson 1995), this did not appear to have a strong negative effect on deer mice after the wildfire.

In addition to our findings on gray-collared and least chipmunks, other researchers have documented positive responses to thinning by chipmunk species (Carey 2000, 2001, Wilson and Carey 2000, Carey and Wilson 2001,

**Table 10.** Model selection results<sup>a</sup> from weighted regression analysis of treatment effects on total small mammal biomass at the Jemez Mountains study area, northern New Mexico, USA, 2001–2003.

Model	AIC <sub>c</sub>	ΔAIC <sub>c</sub>	w <sub>i</sub>	K
Biomass{fire}	−100.831	0.000	0.28	3
Biomass{year}	−100.125	0.706	0.20	4
Biomass{thin + fire}	−98.869	1.962	0.11	4
Biomass{site + fire}	−98.427	2.404	0.09	4
Biomass{constant}	−98.388	2.443	0.08	2

<sup>a</sup> Results include Akaike's Information Criterion corrected for small sample size (AIC<sub>c</sub>), relative AIC<sub>c</sub> (ΔAIC<sub>c</sub>), Akaike weight (w<sub>i</sub>), and number of parameters (K) for models with ≥5% of the w<sub>i</sub>.

**Table 11.** Model-averaged effect sizes, 95% confidence intervals, and relative importance values<sup>a</sup> from weighted regression analysis of treatment effects on total small mammal biomass at the Jemez Mountains study area, northern New Mexico, USA, 2001–2003.

Variable	Effect size	95% CI	Relative importance value
Site <sup>b</sup>			0.21
Yr			0.35
Thin	59.14	–214.25, 332.52	0.23
Fire	66.01	–94.68, 226.69	0.56

<sup>a</sup> Calculated by summing the Akaike weights across all models in which the variable appears.

<sup>b</sup> Site and year effect estimates are blocking effects specific to sites and years, and we do not report them here for the sake of brevity.

Sullivan et al. 2001, Hadley and Wilson 2004). Increased understory vegetation (Carey 2000, 2001) and coarse woody debris (Fitzgerald et al. 1994, but see Hadley and Wilson 2004) may spur these responses. Again, slash retained after thinning appeared to provide focal points for chipmunk activity in our study.

For least chipmunks, the increased availability of food sources, from either forb or pine seeds in the soil bank or aerially applied grass seeds, may have offset the effect of the presumed loss of coarse woody debris after the wildfire, thus explaining the lack of a negative response by chipmunks to wildfire in this study. Krefting and Ahlgren (1974) suggested such a pattern for eastern chipmunks (*Tamias striatus*) in a study of jack pine burns. Carey (2000) also suggested this hypothesis based on research indicating that Townsend's chipmunks (*T. townsendii*) are more common in thinned stands with greater understory vegetation compared to stands with greater amounts of coarse woody debris.

Our results, and those of others (Monthey and Soutiere 1985, Carey and Johnson 1995, Masters et al. 1998, Wilson and Carey 2000, Carey and Wilson 2001, Suzuki and Hayes 2003), indicate that small mammal biomass appears to generally respond positively to thinning disturbances in ponderosa pine and other coniferous forests, assuming the predisturbance habitat is relatively poor (but see Hadley and Wilson [2004], where dominance of the small mammal community by red-backed voles [*Clethrionomys gapperi*] resulted in highest biomass in less disturbed areas). In many low-elevation pine forests of western North America, where deer mice and chipmunks are the dominant species in the small mammal community, positive biomass responses to thinning may be due to an increase in food availability and coarse woody debris. We also documented a positive, though not strong, response of total biomass to wildfire.

Difficulties in conducting large-scale habitat experiments include problems with relevance of the spatial and temporal scale of treatment and monitoring, as well as insufficient experimental design, including a lack of randomization or replication (Smith 1999, Block et al. 2001). We confronted many of these issues during the design and implementation of this multidisciplinary study. The thinned areas at the SPSA were approximately 24 ha in area at each study site,

while at the JMSA the single thinned experimental unit represented approximately half that area. Although the sizes of the treatments represent a significant improvement over experimental treatments that have been criticized for being overly small (e.g., see Smith's [1999] analysis of Von Trebra et al. [1998]), information on larger treated units with reduced potential for edge effects would serve as a useful comparison to our results. The temporal scale was also limited, and continued monitoring of these and other experiments will be necessary to understand long-term responses to treatments. Populations may change with time since treatment as successional sequences move forests toward conditions similar to pretreatment conditions, similar to historic conditions, or into entirely novel conditions. Finally, because treatments were not always randomly assigned to experimental units, the design is more correctly termed quasi-experimental (Block et al. 2001).

Despite the limitations of the FFS study for inference about wildlife responses, we believe our results are robust predictions of short-term small mammal density responses to thinning and wildfire in southwestern ponderosa pine forests. The strength of our analytic approach is that it provides a statistically rigorous and efficient method for modeling changes in population densities across space and time. While the majority of past work on small mammal responses to forest management employed indices of abundance as response variables (e.g., Tester 1965, Bock and Bock 1983, Masters et al. 1998, Steventon et al. 1998, Wilson and Carey 2000, Carey 2001), inference from abundance indices rests on the assumption that the probability of detecting animals is constant across space and time (Nichols 1992, Anderson 2001). This assumption would certainly have been invalid in this case, given our finding that treatments impacted not just densities of small mammals, but capture probabilities and movements as well. Therefore, we believe that the approach of estimating small mammal densities through mark–recapture and MMDM methods leads to more reliable inference. Finally, the emphasis we placed on multi-model inference increases the robustness of the estimated treatment effects.

## Management Implications

The 2003 Healthy Forests Restoration Act (One Hundred Eighth Congress 2003) encourages the use of selective thinning for managing wildfire risk and meeting ecological goals in many forests throughout the United States. Therefore, forest managers will increasingly find themselves in the position of evaluating the appropriateness of thinning treatments. If managers of southwestern ponderosa pine forests are concerned with maintaining or enhancing small mammal populations (e.g., in areas managed for raptor foraging), our findings indicate that management attention should focus on reducing fuel loads and opening canopies in forest stands with the densest structure, rather than in forests with larger, more widely spaced trees. When managing for predators, managers must balance the application of thinning treatments to increase small

mammal biomass against additional habitat needs of the predator species of interest (e.g., denser closed-canopy stands to facilitate goshawk fledgling survival; Reynolds et al. 1996, Long and Smith 2000). Finally, slash retention after thinning will also likely enhance small mammal populations. In all cases, site-specific analysis and monitoring will be critical to making appropriate decisions about treatment application (Block et al. 2001, Brown et al. 2004).

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## Appendix A. Computation of Akaike Information Criterion corrected for small samples (AIC<sub>c</sub>) for model selection in weighted regression analysis.

Computation of the vector of effect sizes ( $\hat{\beta}_i$ ) and variance–covariance matrix effects ( $\hat{\Sigma}_i$ ) for each model ( $i$ ) in a weighted regression analyses follows from Draper and Smith (1998) as

$$\hat{\beta}_i = (X_i V^{-1} X_i)^{-1} X_i V^{-1} Y \quad (1)$$

and

$$\hat{\Sigma}_i = (X_i V^{-1} X_i)^{-1} \hat{\sigma}_i^2, \quad (2)$$

where  $X_i$  is the design matrix of model  $i$ ,  $V$  is the variance–covariance matrix of the model-averaged density estimates,  $Y$  is the vector of model-averaged density estimates, and

$\hat{\sigma}_i^2$  is estimated from the residual sum of squares of the model, divided by the appropriate degrees of freedom, resulting in an unbiased estimator,

$$\hat{\sigma}_i^2 = \frac{(Y - X_i \hat{\beta}_i) V^{-1} (Y - X_i \hat{\beta}_i)}{(n - K_i)} \quad (3)$$

where  $n$  is the sample size of  $Y$  estimates and  $K_i$  is the number of parameters in model  $i$  plus 1 for the estimation of  $\hat{\sigma}_i^2$ .

Integral to estimating AIC for model  $i$  is the recognition that the joint likelihood function for  $\beta_i$  and  $\sigma_i^2$  is given by

$$\begin{aligned} \mathfrak{L}(\beta_i, \sigma_i^2 | Y, X_i, V) \\ = \frac{1}{\sqrt{|\sigma_i^2 V|} (2\pi)^n} \\ \exp\left(-\frac{1}{2} (Y - X_i \beta_i) (\sigma_i^2 V)^{-1} (Y - X_i \beta_i)\right). \end{aligned} \quad (4)$$

Substituting the maximum likelihood estimators of  $\hat{\beta}$ , given above, and  $\hat{\sigma}_i^2$ , given as

$$\hat{\sigma}_i^2 = \frac{(Y - X_i \hat{\beta}_i) V^{-1} (Y - X_i \hat{\beta}_i)}{(n)}, \quad (5)$$

into the right side of equation 4 results in a log  $\mathfrak{L}$  function proportional to

$$\log \mathfrak{L}(\beta_i, \sigma_i^2 | Y, X_i, V) \propto -\frac{1}{2} n \log(\sigma_i^2) \quad (6)$$

and AIC is computed, as in Burnham and Anderson (2002), as

$$\text{AIC}_i = n \log \hat{\sigma}_i^2 + 2K_i. \quad (7)$$

Finally, a small-sample size correction (Hurvich and Tsai 1989) is calculated as

$$\text{AIC}_c = \text{AIC} + 2K \left( \frac{n}{n - K - 1} \right). \quad (8)$$

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