NEST TREES OF NORTHERN FLYING SQUIRRELS IN THE SIERRA NEVADA

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We examined the nest-tree preferences of northern flying squirrels (*Glaucomys sabrinus*) in an old-growth, mixed-conifer and red fir (*Abies magnifica*) forest of the southern Sierra Nevada of California. We tracked 27 individuals to 122 nest trees during 3 summers. Flying squirrels selected nest trees that were larger in diameter and taller than either random trees or large (>50-cm diameter at breast height) nearest-neighbor trees. Snags were used more often than live trees relative to their availability. Nest trees were usually close to riparian habitat; 86% of nest trees were <150 m from a perennial creek. Flying squirrels selected red fir and avoided incense cedar (*Calocedrus decurrens*). Mean distances between nest trees and size of core-nest areas were greater for males than for females. No detectable relationship was found between size of core-nest area and distance to a perennial creek. These results suggest that flying squirrels of the Sierra Nevada may require large trees and snags within 150 m of perennial creeks for their critical habitat needs.

Key words: *Glaucomys sabrinus*, nest trees, radiotelemetry, riparian habitat, Sierra Nevada, snags

The northern flying squirrel (*Glaucomys sabrinus*) is a small (100- to 150-g), nocturnal, arboreal mammal that inhabits forests throughout much of northern and western North America (Wells-Gosling and Heaney 1984). As the principal prey species of the California spotted owl (*Strix occidentalis occidentalis*) and the northern spotted owl (*S. o. caurina*—Williams et al. 1992), northern flying squirrels have become an important consideration in forest management decisions. Northern flying squirrels also have received research attention because they frequently consume hypogeous and epigeous fungal sporocarps (truffles and mushrooms, respectively—Pyare and Longland 2001). By consuming fungi, northern flying squirrels assist in the dispersal of mycorrhizal fungi, which in turn are critical for water and nutrient uptake by forest trees (Maser and Maser 1988). Additionally, northern flying squirrels frequently consume and disperse fragments of arboreal lichens (e.g., *Bryoria*—Carey et al. 1999; Hayward and Rosentreter 1994).

Recent studies of the habitat preferences of the northern flying squirrel have identified several patterns of habitat prefer-

ence, den use, and movement. Flying squirrels can occupy both old-growth and second-growth forest stands, including young, managed stands that are 45–70 years old (Carey 1995; Carey et al. 1999). Northern flying squirrels frequently change nest trees or dens, and an individual may use 2–12 dens each season (Carey et al. 1997). Northern flying squirrels prefer to nest in tall and large-diameter trees and snags (Bakker and Hastings 2002; Carey et al. 1997; Cotton and Parker 2000), but in some second-growth stands they may select nest trees as small as 16–20 cm in diameter (Mowrey and Zasada 1984). In addition, this species frequently nests in both dead snags and live trees with cavities and may use either depending on availability (Cotton and Parker 2000; Gerrow 1996; McDonald 1995).

In the drier, southern extent of its geographic range, very little is known about the specific habitat requirements of the northern flying squirrel. The effects of forest thinning on northern flying squirrel densities were studied in the southern Cascade Range of northeastern California (Waters and Zabel 1995) and a general description of the elevation and habitat range of the northern flying squirrel is available for southwestern Utah (Musser 1961). Almost no information exists regarding the habitat requirements of northern flying squirrels in the Sierra Nevada of California.

The purpose of this study was to characterize nest-tree selection by northern flying squirrels in a southern Sierra Nevada old-growth forest. If this species' habitat requirements
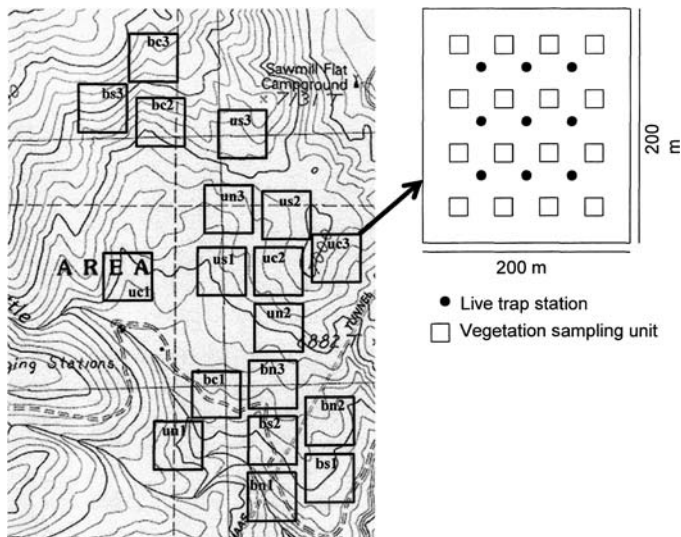
FIG. 1.—Diagram of live-trap and vegetation sampling grids within 18 separate 4-ha forest plots at Teakettle Experimental Forest (Fresno County, California).

are increasingly restricted near the edge of their geographic ranges (Brown 1984; Lomolino and Channell 1995), then it is important to identify the ecological needs for this species in the Sierra Nevada and other southern mountain ranges. Specifically, we examined nest-tree selection by tree type (snag compared to live), tree size (diameter and height), tree species, squirrel sex, and creek association.

MATERIALS AND METHODS

Study area.—Research was conducted at Teakettle Experimental Forest, a 1,300-ha, mixed-conifer and red fir (*Abies magnifica*) forest in the southern Sierra Nevada, Fresno County, California. Teakettle is at 1,800–2,400 m elevation and is characterized by a strongly Mediterranean-influenced montane climate, with hot, dry summers, and precipitation that falls almost exclusively as snow during winter (Major 1990). Average annual precipitation is 110 cm at 2,100 m, and average summer (June–September) rainfall during this study (2000–2002) was 1.0 cm ± 0.4 *SE*. Dominant forest trees included white fir (*Abies concolor*), red fir, sugar pine (*Pinus lambertiana*), Jeffrey pine (*P. jeffreyi*), and incense cedar (*Calocedrus decurrens*). Teakettle Experimental Forest was an unlogged, old-growth forest characterized by a multilayered canopy and numerous large (>100 cm diameter at breast height [dbh]) trees, snags, and decayed logs (North et al. 2002). As part of a long-term study on ecosystem responses to different management strategies, twelve 4-ha study plots outside the primary study area were thinned in August–September of 2000 and July–August of 2001.

Squirrel and nest-tree sampling.—We trapped flying squirrels in 18 separate 4-ha plots from June through August 2000–2002. Each plot consisted of 9 live-traps (Tomahawk Live Trap, Model 201, Tomahawk, Wisconsin) set in a 3 × 3 square grid with 50-m spacing between points and a 50-m buffer zone between points and the plot border. We installed each trap 1.5 m high on the trunk of a large (>70-cm dbh) tree. Traps were baited with a mixture of peanut butter and rolled oats and a small cardboard shelter filled with polyethylene stuffing material was provided for thermal insulation. We checked traps at dawn and dusk. Body mass, sex, reproductive condition, and age class were recorded for all captured squirrels. All study animals were marked with numbered

metal ear tags and fitted with a 2.0- to 3.5-g radiocollar transmitter (<3.5% of body mass; Model MD-2C, Holohil Systems Ltd., Carp, Ontario, Canada). Initially, we anesthetized study animals with methoxyflurane (Metofane; Pitman-Moore, Mundelein, Illinois), but its use was unnecessary and discontinued during the 2nd year of study. Animals recovered quickly from anesthetic and were released within 6 h after sedation. Unanesthetized animals were released immediately. Animals fitted with a radiotransmitter from a previous year were excluded from study in all following years. Research on live animals followed guidelines of the University of California Davis Animal Use and Care Advisory Committee and American Society of Mammalogists (Animal Care and Use Committee 1998).

We located squirrels with an AVM receiver (Model TR-4, AVM Instrument Co. Ltd., Livermore, California). Individuals were tracked during the day and located 1–3 times weekly from June to September in 2000–2002 or until transmitters were recovered. Nest trees were characterized by size (dbh), height (by using a clinometer), species, type (live tree or snag), and frequency of use. We also estimated percentage canopy cover at each nest tree by using a spherical densiometer (mean value of 4 readings taken 1 m away from the base of the tree in each cardinal direction; Model A, Forestry Suppliers, Jackson, Mississippi). In rare cases (4%) where the radiosignal was equally strong between 2 trees, measurements were taken for both trees and mean values were used for analysis. The geographic locations of all nest trees were recorded (±1-m accuracy) in Universal Transverse Mercator (UTM) coordinates by using a Trimble TDC-2 global positioning system unit (Trimble Navigation, Sunnyvale, California).

To test if squirrels selected large trees (relative to other trees in the immediate vicinity) for nest sites, dbh and height also were recorded for the nearest large (>50-cm dbh) tree or snag. Large neighbor trees were selected for statistical comparison (rather than nearest neighbors of any size) for 2 reasons. First, nearest-neighbor trees were adjacent to nest trees, making it more likely that study animals encountered them than randomly selected trees and snags in nearby (25–100 m distance) plots, and 2nd, use of large-diameter (>50-cm dbh) trees ($\bar{X} = 86.3$ cm) rather than random trees ($\bar{X} = 58.4$ cm) in the analysis of tree-size selection was a more conservative test (lower type I error; see "Results"). If there was any doubt as to whether a nearest neighbor might be occupied by the study animal, the next nearest-neighbor tree was used for comparison instead.

To determine availability of live trees, snags, and different tree species, vegetation was sampled in 18 separate 4-ha forest plots within 25–250 m distance of core-nest areas (the area enclosed by an individual's nest trees). Within each plot, sixteen 0.05-ha quadrats were spaced 50 m apart in a 4 × 4 grid (Fig. 1). All quadrats were located ~25 m from live-trap grid points and were located >20 m from the edge of a plot. Within these quadrats, dbh and species were recorded for all trees and snags >5-cm dbh. Percentage canopy cover was estimated from spherical densiometer readings, taken in the 4 cardinal directions and 1 m from the base of random trees (randomly selected from a pooled list of all trees >50-cm dbh within all 0.05-ha quadrats of all forest plots).

We analyzed spatial UTM coordinate data and estimated the distance between nest trees, the size of the core-nest area, and the distance to the nearest perennial creek by using ArcView GIS (Version 3.2a, Environmental Systems Research Institute Inc., Redlands, California). For distances <250 m, the distance of each nest tree to the nearest perennial creek was measured by using a laser rangefinder (±1-m accuracy; Model 500, Bushnell Performance Optics, Overland Park, Kansas). By following the methods of Witt (1992), Gerrow (1996), and Cotton and Parker (2000), the size of each core-nest area was esti-

mated by using the minimum convex polygon method (Mohr and Stumpf 1966).

Statistical analysis.—Single-factor model II analysis of variance was used to test for an effect of sex or year of study on core-nest area, mean distance traveled between nest trees, and the number of nest trees used per month. To examine the potential influence of a sampling intensity bias, Pearson's product-moment correlation was used to examine if a relationship existed between the number of nest trees or size of core-nest areas and the number of times an individual was located (removing all samples with <10 observations).

To determine whether flying squirrels selected larger-diameter and taller nest trees, we compared the dbh and height measurements of nest trees and large nearest-neighbor trees by using a paired *t*-test. An independent *t*-test was used to compare the dbh of nest trees and 122 trees selected randomly from adjacent vegetation sample plots where flying squirrels were regularly captured ($n = 5$ plots). Only nest trees >37-cm dbh (37 cm was the minimum nest-tree dbh in our study) were used in our random sample. Nest trees used by an individual animal only once or occupied by a study animal in a previous year were not used in this and following analyses.

We used Pearson's chi-square (χ^2) to test the null hypotheses that flying squirrels showed no nest preference based on the type (snag versus live tree) or species of tree. Another χ^2 test was used to test whether a difference existed in the proportion of snags versus live trees among different species of nest trees. Tree availability data in these tests were obtained from the five 4-ha vegetation sample plots described above. To investigate and possibly remove the effect of tree size, this analysis was conducted by using trees >37-cm dbh (representing 100% of nest trees) in a 1st test and trees >70-cm dbh (representing >95% of nest trees) in a 2nd test. Because results of these tests were statistically similar, only results for the latter analysis were reported. In addition, 95% confidence intervals were calculated based on a Bonferroni *z* statistic for the observed proportion of use of each tree species (by using available trees >70-cm dbh) to evaluate tree species preferences by flying squirrels (Neu et al. 1974).

An unpaired *t*-test was used to determine whether nest trees were closer to creek areas than were randomly selected trees. A total of 122 random trees was selected from a series of random UTM coordinates within our 400-ha mapped study site. We used an independent *t*-test to determine whether percentage canopy cover of nest trees was different from the cover of randomly selected trees from nearby sample plots.

All variables were tested for normality with the Kolmogorov–Smirnov test and for homoscedasticity with Levene's test. Core-nest area was log-transformed to meet assumptions of parametric tests. All statistical tests were conducted with Statistica (Version 6.1, StatSoft Inc., Tulsa, Oklahoma), and differences were considered significant when $P < 0.05$.

RESULTS

We radiocollared 27 flying squirrels (2000: 5 males, 2 females; 2001: 6 males, 3 females; and 2002: 3 males, 8 females) and located them 434 times to 122 nest trees. The mean $\pm$ *SE* number of nest trees used per flying squirrel was 5.4 ± 0.4 (range: 3–9). The size of core-nest areas varied between sexes ($F = 4.545$, *d.f.* = 1, 17, $P = 0.048$) but not years ($F = 2.031$, *d.f.* = 1, 17, $P = 0.172$). The mean distance between nest trees also was different between sexes ($F = 10.100$, *d.f.* = 1, 17, $P = 0.006$) but not years ($F = 0.001$, *d.f.* = 1, 17, $P = 0.995$). The number of nest trees used per month was different between years ($F = 15.679$, *d.f.* = 1, 14,

TABLE 1.—Differences between male and female northern flying squirrels in the number of nest trees used per month, core-nest area, and mean distance between nest trees (Teakettle Experimental Forest, California; 2000–2002). In all cases, $n = 8$ for males and $n = 11$ for females (data pooled between years; only individuals located >10 times are presented), except the number of nest trees used per month for males ($n = 5$).

Dependent variable	Sex	Mean	*SE*	Range
Nest trees used per month (*n*)	Male	4.75	0.90	2.98–7.58
	Female	3.52	0.38	1.85–6.34
	Combined	3.90	0.40	1.85–7.58
Core-nest area (ha)	Male	2.20	0.59	0.21–4.42
	Female	0.87	0.29	0.29–3.52
	Combined	1.43	0.33	0.21–4.42
Mean distance between nest trees (m)	Male	166.9	35.4	20.0–323.5
	Female	68.2	7.4	41.4–121.7
	Combined	109.7	18.8	20.0–323.5

$P = 0.001$) but not sexes ($F = 2.261$, *d.f.* = 1, 17, $P = 0.155$). Although no differences were found in number of nest trees used per month between males and females, males had larger core-nest areas and traveled greater distances between nest trees than females (Table 1). No correlation was found between the number of times an individual was located and the number of nest trees used per month ($r = 0.003$, $P = 0.850$) or the size of core-nest area ($r = 0.116$, $P = 0.197$).

The dbh of nest trees (121.0 cm $\pm$ 3.2 *SE*) was larger than that of large nearest-neighbor trees (86.3 $\pm$ 2.4 cm; $t = 10.05$, *d.f.* = 101, $P < 0.001$). Also, the height of nest trees (40.2 m $\pm$ 1.3 *SE*) was larger than that of large nearest-neighbor trees (30.0 $\pm$ 1.4 m; $t = 7.19$, *d.f.* = 101, $P < 0.001$). Nest trees also were larger in dbh than random trees (61.6 cm $\pm$ 2.1 *SE*; $t = 16.192$, *d.f.* = 202, $P < 0.001$); only 18.9% of nest trees were <100-cm dbh.

Relative to their availability (11% snags and 89% live trees), snags ($n = 46$) were more commonly selected for nest trees than were live trees ($n = 76$; $\chi^2 = 60.44$, *d.f.* = 1, $P < 0.001$). Species composition of nest trees also differed from that of larger (>70-cm dbh), random trees ($\chi^2 = 9.61$, *d.f.* = 4, $P = 0.048$). Red fir was used more often than expected, whereas incense cedar was selected less often (Table 2). No difference was found in the proportion of snags versus live trees among different species of nest trees ($\chi^2 = 1.770$, *d.f.* = 4, $P = 0.778$).

Nest trees were closer to creeks than were random trees ($t = -9.66$, *d.f.* = 236, $P < 0.001$). The mean distance of a nest tree to a perennial creek at our study site was 110.9 m versus 500.7 m for random trees. Eighty-six percent of nest trees were within 150 m of a creek (Fig. 2). Canopy cover of nest trees (61.8% $\pm$ 1.8 *SE*) was similar to that of random trees (62.8 $\pm$ 1.7%) from adjacent forest habitat ($t = -0.497$, *d.f.* = 236, $P = 0.619$).

DISCUSSION

Core-nest areas.—Our results were consistent with those of other studies of flying squirrels, showing that males have larger

TABLE 2.—Percentage tree use by northern flying squirrels versus availability of common tree species at Teakettle Experimental Forest (California). Only trees with >70-cm diameter at breast height were used for the calculation of tree availability. Calculation of 95% confidence intervals was based on a Bonferroni z statistic. Differences ($P < 0.05$) in observed and expected frequencies are indicated by an asterisk (*).

| Species	% den trees	95% CI[a]	Expected %
White fir	53.7	42.0−65.3	61.9
Red fir	17.1*	8.3−25.8	6.6
Jeffrey pine	10.6	3.4−17.7	12.2
Sugar pine	17.1	8.3−25.8	11.1
Incense cedar	1.6*	0.4−4.6	8.3

[a] *CI*, confidence interval.

FIG. 2.—Distribution of northern flying squirrel nest-tree distances to the nearest perennial creek ($n = 122$) at Teakettle Experimental Forest (Fresno County, California), 2000–2002. The percentage of nests in each distance class is presented in parentheses above each bar.

home ranges and travel greater distances than females (Cotton and Parker 2000; Gerrow 1996; Martin and Anthony 1999), and that both sexes use similar numbers of nest trees (Carey et al. 1997, Cotton and Parker 2000). Male flying squirrels in our study may have traveled greater distances between nests to gain greater access to mates (Gerrow 1996; Martin and Anthony 1999).

Summer core-nest areas of flying squirrels at our southern Sierra Nevada study site were smaller than winter core-nest areas in northwestern British Columbia, Canada (3.7 ha ± 0.9 *SE* and 1.4 ± 0.4 ha for males and females, respectively—Cotton and Parker 2000). Home ranges of flying squirrels in Oregon (Martin and Anthony 1999; Witt 1992) and New Brunswick, Canada (Gerrow 1996) were slightly larger than the core-nest areas of the animals of this study. These latter 2 comparisons are not surprising because an individual's core-nest area does not incorporate all of its foraging areas and is smaller than the size of its home range (Cotton and Parker 2000).

The average number of nest trees used per month by flying squirrels was greater in this study than in the coast range of Oregon (2.1—Carey et al. 1997) and northwestern British Columbia (2.2—Cotton and Parker 2000), but less than in interior Alaska (5.0—Mowrey and Zasada 1984). Use of multiple nests by flying squirrels may reduce the risk of predation and parasitism, facilitate social interactions, or increase foraging efficiency on truffles, a preferred but highly variable resource over seasons and across habitats (Carey et al. 1997).

Nest-tree characteristics.—Consistent with results from other studies, we found northern flying squirrels in old-growth forests generally selected larger trees and snags for nesting. Northern flying squirrels also selected larger-diameter residual snags in managed and old-growth forests of western and central Oregon (Carey et al. 1997; Martin 1994); larger-diameter nest trees in New Brunswick (Gerrow 1996), southwestern Washington (Clark 1995), and southeastern Alaska (Bakker and Hastings 2002); and larger-diameter, taller, and older trees in northwestern British Columbia (Cotton and Parker 2000). Larger trees and snags may benefit flying squirrels by providing more cavities for nesting (Carey et al. 1997), greater thermal insulation (Jeffrey 2000), reduced predation risk (Carey et al. 1997; Harestad 1990), and an increased biomass of the forage lichen *Bryoria fremontii* (T. Rambo, pers. comm.).
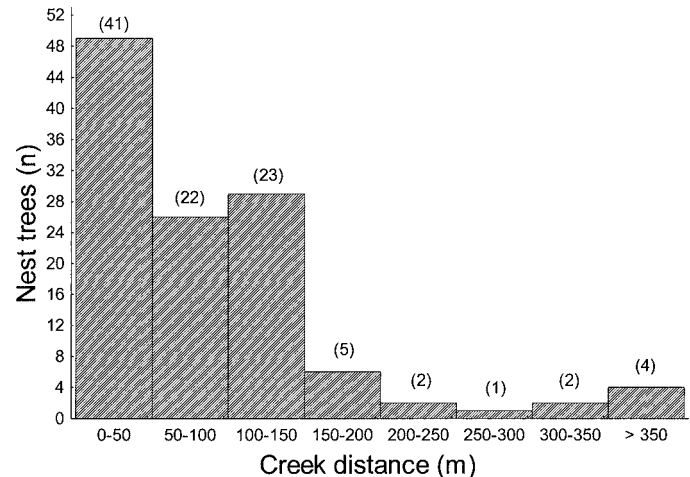
Flying squirrels preferred snags over live trees in our study. Nearly 40% of nest trees used by flying squirrels were snags, although snag availability at our site was relatively low. Flying squirrels most likely select snags because they offer more cavities for nesting than do live trees (Meyer 2003). In western Oregon (Carey et al. 1997), southwestern Washington (Clark 1995), and Alberta, Canada (McDonald 1995), flying squirrels preferred to nest in large, residual snags rather than live trees, particularly in managed second-growth forests where snags and large trees were rare. Flying squirrels also preferentially used snags and trees with bole entries and dead tops in southeastern Alaska (Bakker and Hastings 2002). In contrast, very few flying squirrels in subboreal forests of northwestern British Columbia used snags as nest trees (Cotton and Parker 2000). This finding likely reflected the relatively young age of forest stands at the latter site and related low abundance of snags. Thus, flying squirrels frequently use and often select snags over live trees when a sufficient number of snags is present.

Flying squirrels at our study site strongly favored nest trees near perennial creeks. Flying squirrels are frequently associated with the presence of surface water (streams and swamps), perhaps because both truffles and mushrooms are abundant in these areas (Heaney 1999). Individuals near creeks have greater access to drinking water and truffles than do residents of neighboring upland areas (Meyer 2003). Cotton and Parker (2000) also noted that northern flying squirrels in British Columbia tended to use nest trees in mesic and mesic–wet areas. Flying squirrels near the arid southern extent of their range possibly are strongly constrained by the presence of riparian habitat that contains adequate food resources.

Flying squirrels selected red fir and avoided incense cedar nest trees. Flying squirrels may select red fir because this species harbors a greater abundance of *B. fremontii* (a frequent food item in the diet of flying squirrels in this study—M. Meyer, in litt.) than all other tree species at Teakettle (T. Rambo, pers. comm.). Alternatively, red fir may be selected because it is

preferred by some species of cavity excavators (e.g., wood-peckers), although this has not been observed in other regions of the Sierra Nevada (e.g., Raphael and White 1984). It is not clear why flying squirrels avoided incense cedar, although incense cedar contains high levels of volatile terpenes (Von Rudloff 1981) that are odoriferous and may be repulsive to this species. Alternatively, incense cedar may have lower invertebrate abundance causing them to be avoided by cavity excavators, and consequently have fewer suitable nest cavities than other tree species.

Management implications.—Although flying squirrels exhibited flexibility in selection of nest-tree characteristics in other studies (e.g., Cotton and Parker 2000; Mowrey and Zasada 1984), the nest-tree preferences of flying squirrels in our study highlight the potential importance of retaining larger-diameter snags and live trees in Sierra Nevada forests. Silvicultural practices that remove a substantial portion of these key structural forest components (e.g., clear-cutting and shelter-wood thinning) may negatively impact flying squirrel populations by reducing both nest sites and forage biomass (Carey 2000; Waters and Zabel 1995; Witt 1992). In addition, our results emphasize the value of riparian habitat to the northern flying squirrel in more xeric forest regions. Forest areas within 150 m of even small (<1-m-wide) perennial creeks were important habitat elements to northern flying squirrels and recent studies have indicated this to be true for other species of wildlife as well (Erman et al. 1977; Erman and Mahoney 1983; Vesley and McComb 2002). Current management plans in the Sierra Nevada (e.g., United States Department of Agriculture Forest Service 2002) call for 30-m-wide buffer strips along riparian corridors. We believe these recommendations could be inadequate to protect northern flying squirrels and those species dependent on them.

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