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HOME RANGE CHARACTERISTICS OF GREAT GRAY OWLS IN YOSEMITE NATIONAL PARK, CALIFORNIA

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Abstract.—We studied home range and habitat use of radio-tagged Great Gray Owls (*Strix nebulosa*) in Yosemite, California. From 1986–90 we made 5338 relocations on nine adult and three juvenile owls. Home-range size was not correlated with number of locations and was significantly different between breeding and nonbreeding periods. Breeding female summer home range averaged 61.47 ha and during the winter 2457.27 ha, while males average 19.89 and 2112.87 ha, respectively. Juveniles and nonbreeding birds had home-range sizes intermediate between seasonal values of breeding owls. Home ranges for California Great Gray Owls were larger than has been recorded for all studies in North America, but smaller than in Europe. All owls were found to have intensive high-use activity centers ($\bar{x}$ = 17.56 ha) in summer, with use patterns influenced primarily by meadows. Over 60% of all relocations occurred within 100 m of a meadow. Great Gray Owls habitat usage during summer was concentrated in fir (*Abies* spp.) and lodgepole (*Pinus contorta*) habitat types, while during the winter, birds moved to lower elevations into Sierra mixed conifer habitats. This post-breeding movement was the cause of the large nonbreeding home ranges. During winter, paired birds did not remain together, even though all birds moved to lower elevation habitats below deep snow-pack levels. We suggest that Great Gray Owls in California have responded to the relatively hot and southern habitat with unique adaptations that have allowed several local populations to persist within the upper montane Sierra Nevada forest zone. The protection of meadow foraging habitat, as well as nesting locations, will be important for the continued preservation of this southernmost North American population of Great Gray Owls in Yosemite National Park.

Key Words: *Great Gray Owl*; Strix nebulosa; *home range*; *habitat use*; *California*; *Yosemite National Park.*

CARACTERÍSTICAS DEL ÁMBITO DE HOGAR DE *STRIX NEBULOSA* EN EL PARQUE NACIONAL YOSEMITE, CALIFORNIA

Resumen.—Estudiamos el uso del hábitat y ámbito de hogar de *Strix nebulosa* utilizando radiotransmisores en Yosemite, California. Realizamos 5338 localizaciones de 9 individuos adultos y tres juveniles entre 1986 y 1990. El tamaño del ámbito de hogar no se correlacionó con el número de localidades y fue significativamente diferente entre los periodos reproductivo y no reproductivo. El ámbito de hogar de las hembras tuvo una extensión promedio de 61.47 ha durante la época reproductiva y de 2457.27 ha durante el invierno, mientras que para los machos los promedios fueron 19.89 y 2112.87 ha, respectivamente. Los juveniles y los adultos no reproductivos tuvieron tamaños de ámbito de hogar intermedios entre los valores estacionales observados para individuos que se encontraban criando. Los tamaños de ámbito de hogar estimados para *S. nebulosa* en California fueron mayores que los que se han encontrado en todos los demás estudios realizados en Norteamérica, pero menores que los encontrados en Europa. Se encontró que todos los búhos tienen centros de actividad intensiva ($\bar{x}$ = 17.56 ha) en el verano, con patrones de uso influenciados primariamente por los prados húmedos. Más del 60% de las localizaciones ocurrieron a menos de 100 m de un prado. El uso del hábitat por parte de *S. nebulosa* durante el verano se concentró en hábitats dominados por abetos y *Pinus contorta*, mientras que en el invierno más buhos se trasladaron a elevaciones más bajas, hacia hábitats mixtos de coníferas de sierra. Este movimiento posterior a la reproducción causó los altos valores de tamaño de ámbito de hogar durante el

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invierno. Durante el invierno, los búhos con pareja no permanecieron juntos, aunque todos los búhos se trasladaron a hábitats menos elevados que aquellos con capas profundas de nieve. Sugerimos que, en California, *S. nebulosa* ha respondido al ambiente relativamente cálido y meridional con adaptaciones únicas que han permitido que varias poblaciones locales persistan dentro de la zona superior boscosa de la Sierra Nevada. La protección de los prados que constituyen su hábitat de forrajeo, así como de los lugares de anidación, será importante para la supervivencia continua de ésta, la población norteamericana más meridional de *S. nebulosa*.

[Traducción de los autores revisada por el equipo editorial]

The southernmost population of Great Gray Owls (*Strix nebulosa*) in North America occurs in California, with birds found only in habitats of the Sierra Nevada and Cascade ranges in the east-central portion of the state (Winter 1986, Bull and Duncan 1993). Because of their restricted range, information is needed to guide habitat management of this endangered species in California, particularly in relationship to habitat associations and movement patterns. Radiotelemetry can provide a relatively cost-efficient, accurate, and precise methodology to gain insight into wildlife movement and habitat use (White and Garrott 1990), especially for difficult to detect species such as owls.

In North America and Europe, Great Gray Owls are irruptive (Mikkola 1983, Bull and Duncan 1993). These large scale movements, which often occur in response to food shortage (Nero 1980), complicate home-range calculations. In non-irruptive years, home-range size appears to be fairly consistent among Great Gray Owl populations of North America and Europe. Birds are frequently found to remain within a home range in one general area throughout the year, hunting through the snow during the winter (Nero 1980, Franklin 1988). In eastern Oregon, Bull and Henjum (1990) did find that some owls moved to different locations in the winter. In California there is presently no evidence that Great Gray Owls exhibit irruptive behavior, but owls are known to abandon breeding areas following heavy snowfall (Winter 1985).

We studied seasonal movements and habitat associations of radio-tagged Great Gray Owls, from 1986–90 within the Yosemite region of California. Our objectives were to: (1) estimate home-range size for the Great Gray Owl; (2) compare seasonal home-range sizes among male and female breeding and nonbreeding adults and juveniles; (3) identify position and size of activity centers located within owl home ranges; and, (4) describe vegetation community associations found within Great Gray Owl home ranges.

STUDY AREAS

This study was conducted within Yosemite National Park, in the central California Sierra Nevada Mountains of California. The park is over 300 000 ha in size, with 94% designated as wilderness. Elevations range from 600 m along the Merced River on the western boundary to 4000 m at the Sierra crest. The Sierra Nevada Mountains are a strongly asymmetric range, with a gentle western slope, but a steep eastern escarpment (Huber 1987). Massive granite intrusions dominate the central part of the range, while metamorphic and meta-sedimentary rocks are common on the western slope edges (Huber 1987). Yosemite has a Mediterranean climate with hot, dry summers and cold, moist winters (Elford 1970). Temperatures range from a mean minimum of −1°C in January at the high elevations to a mean maximum of 32°C in July at the low elevations. Normal annual precipitation also varies with elevation from 810 mm at the western boundary to a maximum of 1200 mm at 2600 m elevation. Precipitation generally occurs from November through March, primarily as snow at the mid- and higher-elevations.

Vegetation communities within Yosemite respond to climate and topography with shrub woodlands in the foothills, lower and upper montane forests at the mid-elevations, and subalpine forests interspersed with alpine meadows near the crest (Table 1). The lower and upper montane forests, consisting primarily of conifers, cover 72%, shrubs (foothill woodland) another 5%, and nonvegetated areas cover 17% of the Yosemite region. Meadows and grasslands are distributed within the forests and constitute 4% of the area, while riparian areas cover only 2%.

Great Gray Owls are known to occur primarily in the upper and lower montane zones (Table 1) in areas where there are numerous wet meadows. In Yosemite, these areas include, but are not limited to, Crane Flat, Ackerson Meadow, Hodgdon Meadow, Big Meadow, and McGurk Meadow (Fig. 1).

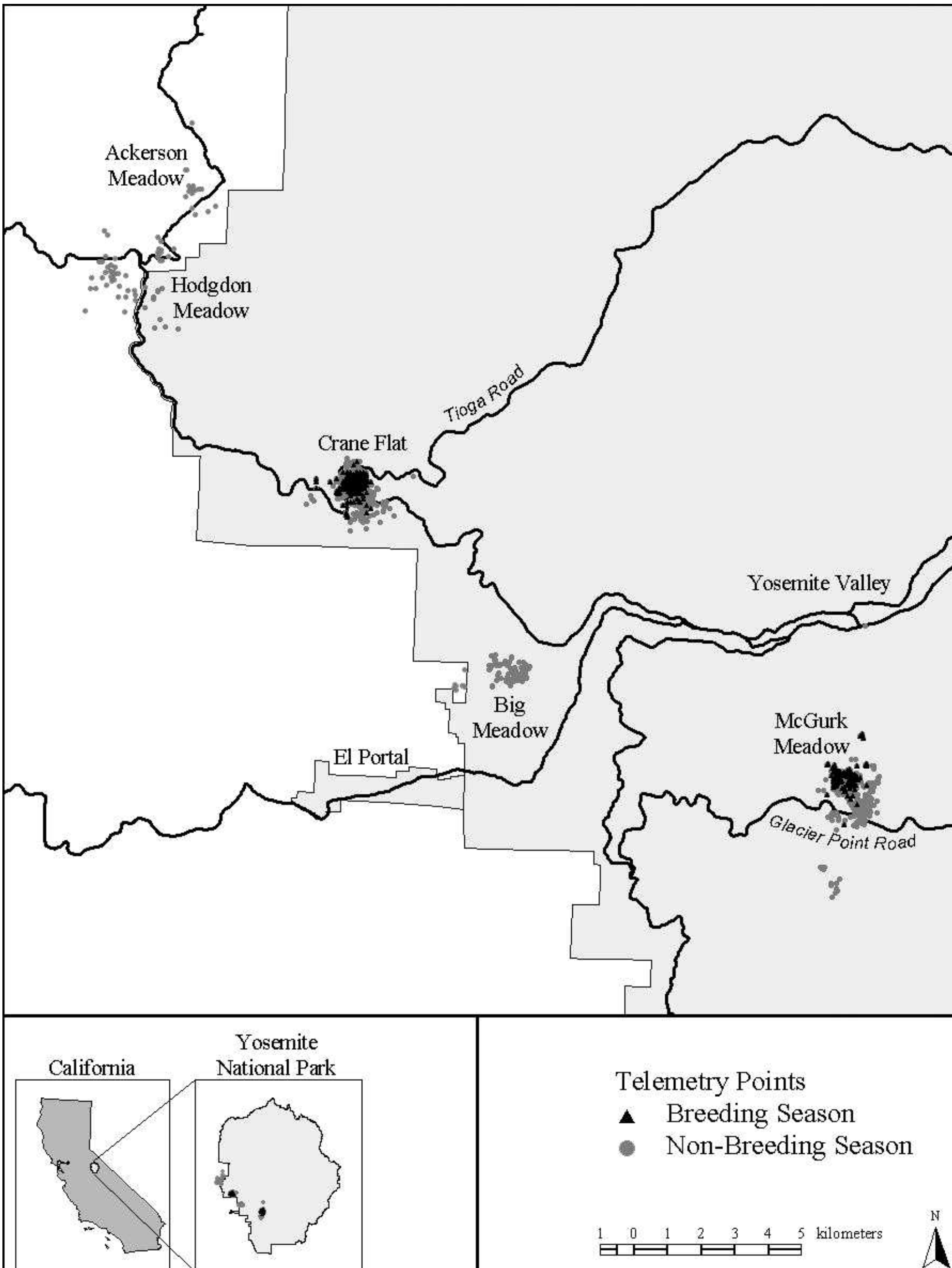

Figure 1. Location of telemetry observations of Great Gray Owls during 1986–90 in Yosemite National Park, California. Breeding season relocations are identified by triangles, while nonbreeding season locations are circles. The park boundary is identified by the narrow black line, while major roads are darker colored lines.

Table 1. Wildlife habitat types and characteristic plant species (based on Mayer and Laudenslayer 1988) for vegetation zones in the Yosemite region of California. Relative Great Gray Owl abundance values and information on areas frequented by Great Gray Owls provided by a Yosemite park-wide survey (C. van Riper III, M. Reid, S. Skiff, M. Sogge, A. Wildman, and J. Winter unpubl. data).

Vegetation Zone	Great Gray Owl	Characteristic Plants	
Wildlife Habitat Type	Relative Abundance[a]	Common Name	Latin Name
Foothill woodland	**Common in winter**		
Mixed chaparral	I	Wedgeleaf ceanothus	*Ceanothus cuneatus*
		Whiteleaf mazanita	*Arctostaphylos viscida*
Montane hardwood-conifer	C	Interior live oak	*Quercus wislizeni*
		Foothill pine	*Pinus sabiniana*
Chamise-redshank chaparral	I	Chamise	*Adenostoma fasciculatum*
Lower montane forest	**Common in summer and winter**		
Ponderosa pine	I	Ponderosa pine	*Pinus ponderosa*
Sierra Nevada mixed conifer	C	Ponderosa pine	*Pinus ponderosa*
		Incense-cedar	*Calocedrus decurrens*
		Giant sequoia	*Sequoiadendron giganteum*
		Sugar pine	*Pinus lambertiana*
White fir	C	White fir	*Abies concolor*
Montane hardwood	U	Canyon live oak	*Quercus chrysolepis*
		California black oak	*Quercus kelloggii*
Wet meadow	C	Bistort	*Polygonum bistortoides*
Urban	U	Ponderosa pine	*Pinus ponderosa*
Upper montane forest	**Common in summer**		
Red fir	C	Red fir	*Abies magnifica*
Jeffrey pine	C	Jeffrey pine	*Pinus jeffreyi*
Montane riparian	I	Willow	*Salix* sp.
Montane chaparral	U	Whitethorn	*Ceanothus cordulatus*
		Greenleaf manzanita	*Arctostaphylos patula*
Wet meadow	C	Tufted hairgrass	*Deschampsia caespitosa*
Lodgepole pine	I	Lodgepole pine	*Pinus contorta*
Sparsely vegetated	U		

[a] U = Uncommon, I = Infrequent, and C = Common.

Birds are also known to occur in the lower montane zone throughout the year (Winter 1986).

METHODS

We identified areas within Yosemite National Park that could potentially contain Great Gray Owls using information from Winter's (1985) preliminary analysis of California Great Gray Owl distributional patterns. We designed our research to survey and capture a representative sample of owls within the central portion of Yosemite, along an elevational gradient from foothill shrub woodlands on the western park boundary, through the lower and upper montane forests at the mid-elevations, to subalpine forest meadows near the Sierra crest. We used the two major park roads (Tioga Pass and Glacier Point) as staging areas for survey and capture of owls (Fig. 1). Yosemite has 356 known meadows (NPS 2003a); we surveyed 221 meadow systems (C. van Riper unpubl. data) and attempted to trap owls at 25 locations.

In order to assure a representative sampling, our trapping design was set to first capture equal numbers of male and female Great Gray Owls at historical breeding locations, then capture birds at representative subsets of vegetation types along the park's entire western elevational gradient. At potential capture locations, from July–August during 1986–89, we used taped Great Gray Owl calls to elicit a response and to pinpoint an owl's location. Bal-chatri traps containing live rodents (Berger and Mueller 1959) were placed directly under the target bird. If the owl did not respond to the trap, a 3.5 m noose pole was used (e.g., Forsman 1980). We also used dho gaza traps and modified verbail trapping techniques (Bloom 1987). Captured owls were restrained, hooded, and a radio-transmitter attached using a nylon back-harness, sewn together with cotton thread where they crossed the breast. Transmitters (Holohill Inc., Carp, ON Canada) were 8.0–8.5 gm and had an average signal life of 12 ± 6 mo.

The sampling design for our radiotelemetry work attempted to balance numbers of diurnal with nocturnal observations. At a minimum, we attempted at least two precise locations per bird per week from the ground for owls in remote locations, while for breeding birds we made daily observations. We attempted to keep sampling levels equal for all owls, but because of inclement weather, owl movements, and deaths, our sampling effort was not spread equally among all radio-tagged birds. Location data were recorded every 10-min, and the time needed between successive observations to generate statistical independence (α = 0.10) was calculated following Swihart and Slade (1985). Furthermore, we limited space-use data from roosting and nesting locations in an effort not to bias home-range patterns, with only one location recorded at these locations until the bird moved. Minimum convex polygon (MCP; White and Garrott 1990) and 75% and 95% adaptive kernel (AK; Worton 1989) estimates of home range were calculated for all radio-tagged owls.

Diurnal tracking was done throughout the year from 1986–90. Diurnal locations of owls were obtained by triangulation of radio signals, followed by visual confirmation. Radio tracking signals were received using TR-1 and TR-2 receivers and hand-held or vehicle mounted H-antennas (Telonics Inc., Mesa, AZ U.S.A.). When tracking remotely from a vehicle, owl locations were repeatedly triangulated along the road corridor in a grid fashion until all triangulations matched. Nocturnal locations were obtained by triangulations of signal compass azimuths from a minimum of three different locations. Nocturnal visual observations were made with night-vision goggles (Rigel 3200, Rigel Optics, Washougal, WA U.S.A.) and headlamps from May–September. During nocturnal periods, each owl was tracked for blocks of 4-continuous hr, spaced across all hours of the night, at least every third day.

The standard deviation of azimuth error was estimated for each meadow area by taking a series of 20 test triangulations using three azimuths to ''fix'' transmitters spaced throughout the area (White and Garrott 1990). This provided an *a priori* estimate of error that was used with subsequent multiple-azimuth triangulated owl locations. Owl UTM locations were estimated using the Maximum Likelihood Length Estimator (MLE) developed by Lenth (1981) and modified by Lee et al. (1985). Only owl fixes with error ellipses $\leq$5.0 ha were used to derive home-range estimates in order to reduce spatial error. We calculated telemetry error using the mean and standard deviation of bearing errors and area of confidence ellipses (Saltz 1994). In addition, relocation error was estimated by placing transmitters at locations unknown to an observer, and then determining distance between estimated and true transmitter position.

We used Pettingill's (1998:261) definition of home range: ''Home range is the total area that a bird habitually occupies.'' We then subdivided the annual home range into ''breeding season'' (15 April–30 September), and the remainder of the year as ''nonbreeding season.'' Birds frequently moved between breeding and wintering areas throughout the nonbreeding period, and it was thus not reasonable to define a ''transition'' home range. Estimates of MCP and AK were generated using the Home Range program (Hooge and Eichenlaub 1997) in ArcView (ArcView Information Software, E.S.R.I., Redlands, CA U.S.A.). Statistically significant differences between MCP and AK home-range size estimates were determined using the paired *t*-test. We used AK 95% and 75% contours to delineate home-range sizes.

The AK 95% estimate is most commonly used to estimate home ranges (Hansteen et al. 1997). However, because Great Gray Owls may focus over half their activity within a small portion of their breeding home range (Bull and Henjum 1990), we *a priori* selected the AK 75% contour to represent each owl's potential activity center when comparing vegetation-type usage. We determined vegetation cover types within Great Gray Owl home ranges, utilizing a Geographic Information System (GIS) that reclassified a vegetation map derived from aerial photographs taken in 1997 (NPS 2003a). We then identified the cover type for each owl relocation, summed locations, and overlaid cover types with home ranges.

RESULTS

Nine adult (5 males, 4 females) and three juvenile Great Grey Owls were captured and radio-tracked from 1986–90. Birds were followed for a minimum of 12 mo unless they died (N = 3), with five birds followed for 1-yr and four birds for 2-yr periods (Table 2). We had sufficient data totaling 5338 independent observations to construct annual home range estimates for seven adult and two juvenile birds (Table 2). Owl home range size was not correlated with the number of locations for AK 95% (r^2 = 0.051, N = 9, P = 0.560) or AK 75% (r^2 = 0.083, N = 9, P = 0.452) within or outside of the breeding season. Home-range size varied an order of magnitude for owls between breeding and nonbreeding periods. For females, the AK 95% home range for the breeding season averaged 61.47 ha, while the nonbreeding season range averaged 2457.27 ha. For the males, the AK 95% home ranges for the breeding and nonbreeding seasons were 19.89 ha and 2112.87 ha, respectively. Nonbreeding adults and juveniles had home ranges intermediate between the seasonal size values of breeding birds (Table 2).

The pattern of spatial use by breeding adult owls revealed that birds utilized activity centers within home ranges (Fig. 2a), with relocations densely packed in localized areas of the home range. The mean size of AK 75% ''activity centers'' for adults that bred was 17.57 ha. These values showed lower variability among the owls than did the AK 95% contours (Table 2). The AK 75% kernels represented groups of owl locations that were centered around nests or roost sites, but also included foraging areas, much as Bull and Henjum (1987) found in Oregon. The breeding season activity centers appeared also to be influenced by topography, vegetation type, and especially meadows, as the AK 75% boundary of the kernel was frequently associated with outer meadow boundaries (Fig. 3). During the nonbreeding period, Great Gray Owl home ranges ($\bar{x}$ = 1220.58 ha) were much larger with multiple activity centers (Fig. 2b). We found

Table 2. Home range size (ha) by Adaptive Kernel (AK) percent probability and breeding status for Great Gray Owls, during 1986–90 in Yosemite National Park, CA. ''Observations'' are the number of independent 10-min locations, while ''Duration of Observations'' is number of consecutive months that the bird was radio-tracked.

Bird Number	Observations	Duration of Observations (mo)	AK Probability 75%	AK Probability 95%
Females that bred—breeding season			Hectares	Hectares
54987	815	21	18.73	59.69
64507	692	12	18.71	49.55
54986	464	19	24.63	75.16
Mean	657	17.3	20.69	61.47
Females that bred—nonbreeding season				
54987	667	21	479.83	977.29
64507	390	12	232.69	854.90
54986	29	19	3417.20	5539.52
Mean	509	17.3	1376.57	2457.27
Male that bred—breeding season				
55000	53	20	8.23	19.98
Male that bred—nonbreeding season				
55000	522	20	752.61	2112.87
Female that did not breed				
54985	987	21	352.77	752.08
Males that did not breed				
24209	262	14	363.07	665.24
64508	90	13	83.90	183.64
Mean	176	13.5	223.49	374.44
Juvenile birds combined				
54988-9	367	30	101.17	350.16

that four of eight Great Gray Owl home ranges spatially overlapped.

Seasonal movements of individual Great Gray Owls showed considerable variability, and pairs did not remain together over the winter period. During the winter, birds that had been paired during the summer used roost sites separated by several km, until they returned to their breeding areas in late February. For example, one female owl moved 25 km southeast and wintered at a relatively high (2900 m) elevation site in the Sierra mixed conifer habitat type, while her mate wintered below 2000 m elevation. Another male owl traveled 20 km south and wintered in open oak-shrub habitat (1280 m elevation), while his female wintered above 2000 m elevation in Sierra mixed conifer. Both pairs returned as mates to previous summer ranges (1987 and 1965 m elevation, respectively) at the onset of the next breeding season.

Habitat types that Great Gray Owls utilized for breeding in Yosemite were primarily Lower- and Upper Montane Forest (Table 1). Most breeding females that we studied nested where red fir (*Abies magnifica*) was the most common habitat type (e.g., Fig. 3). Other female Great Gray Owls used home ranges (e.g., McGurk Meadow) dominated by lodgepole (*Pinus contorta*). Additional montane-forest habitat types used by breeding female owls included Sierra mixed conifer, montane riparian, and montane chaparral types (Table 3).

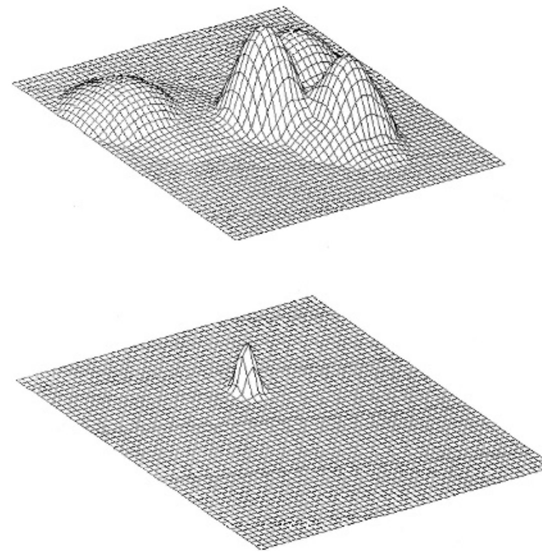

Figure 2. Activity centers of the McGurk female Great Gray Owl during the 1987 breeding period (Bottom; N = 1482 observations) and 1988 nonbreeding period (Top; N = 987) in Yosemite National Park. The basal axes are UTM coordinates while the vertical axis is the number of relocations at each pair of UTM coordinates.

During the nonbreeding season, there was a shift in dominant habitats for the breeding females, as home-range size increased after owls moved to lower elevation meadows (Table 3). These winter areas were dominated by Sierra mixed conifer habitat, interspersed with montane and mixed chaparral (e.g., Ackerson and Big Meadow areas). The Big Meadow area burned with a severe wildland fire in 1990, and by 1997 much of the Sierra mixed conifer type was replaced with either mixed chaparral or montane hardwoods. Even though nonbreeding winter home ranges encompassed different habitat types, like the breeding season, the nonbreeding home ranges were centered on wet meadows.

We found that male Great Gray Owl home ranges included red fir, wet meadow, Sierra mixed conifer,

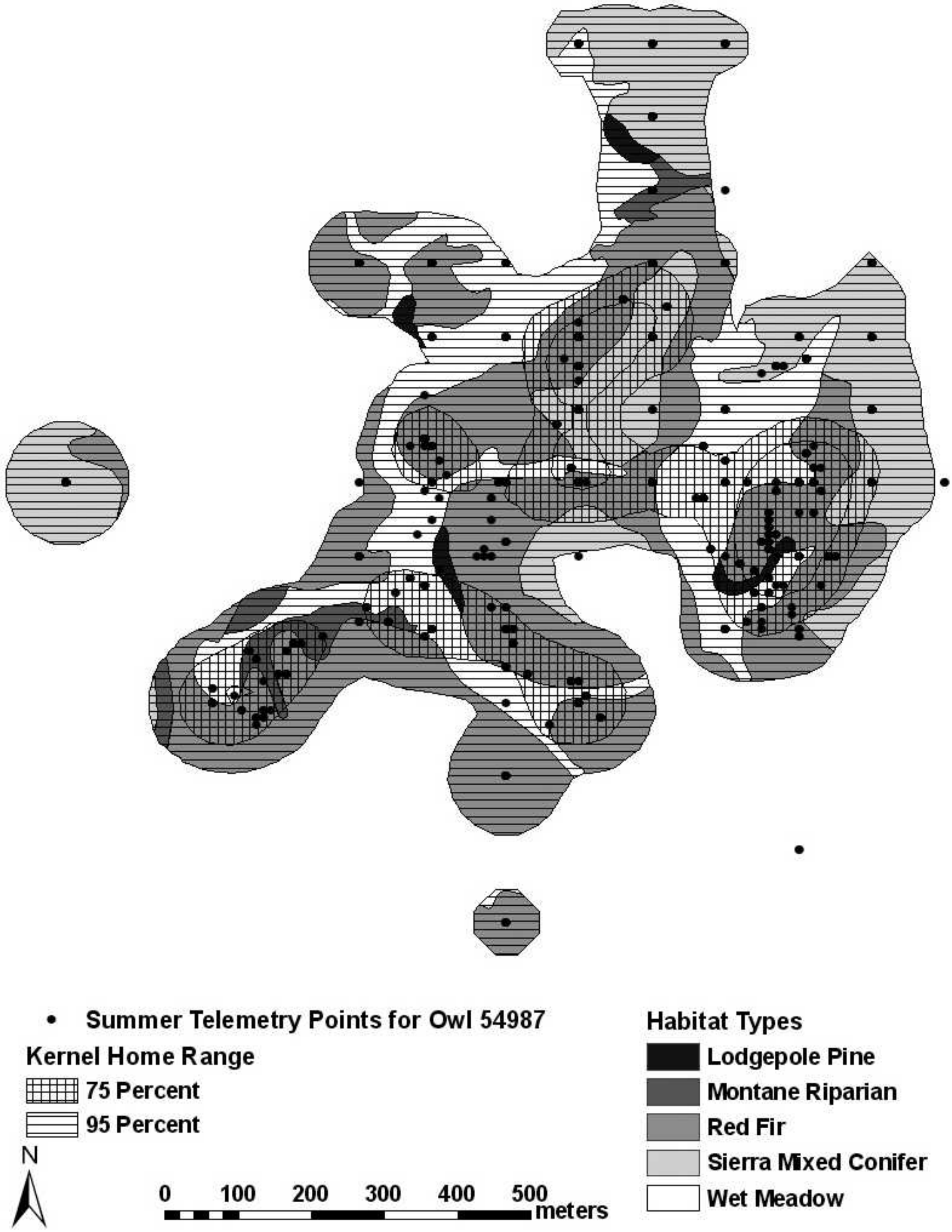

Figure 3. Vegetation cover types within the 95% (outer contour line) and 75% (inner contour line) adaptive kernel home ranges for breeding female Great Gray Owls at Crane Flat during the 1987–89 breeding seasons.

and lodgepole pine habitat types (Table 4). All males that bred moved to lower elevations (e.g., Ackerson and Hodgdon meadows) during the nonbreeding season. The habitat type preferred by male owls during the nonbreeding period was dominated by Sierra mixed conifer.

Cover types within home ranges of the nonbreeding females, nonbreeding males, and juveniles

Table 3. Area of vegetation cover types (Mayer and Laudenslayer 1988) occupied during the 1987–88 breeding and nonbreeding seasons for female Great Gray Owls that bred in Yosemite National Park, CA. Area is given in ha, for adaptive kernel 75% and 95% home range contours.

	OWL NUMBER					
	54987		64507		54986	
COVER TYPE	75%	95%	75%	95%	75%	95%
			Breeding Season			
Lodgepole pine	0.29	0.81	0.35	0.57	10.44	25.59
Montane riparian	0.61	1.81	0.08	1.17	0.00	0.37
Montane chaparral	0.00	0.00	0.00	0.46	0.00	0.00
Red fir	10.19	27.48	8.83	23.56	5.06	28.07
Sierra mixed conifer	2.80	14.7	2.61	11.36	0.00	0.00
Wet meadow	4.84	14.89	6.84	12.43	9.13	21.13
Total (ha)	**18.73**	**59.69**	**18.71**	**49.55**	**24.63**	**75.16**
			Nonbreeding Season			
Chamise chaparral	0.00	0.00	0.00	0.00	0.00	0.05
Jeffrey pine	2.83	5.74	2.13	2.82	107.47	337.41
Lodgepole pine	1.20	1.20	0.90	1.20	529.04	674.96
Mixed chaparral	0.00	0.00	0.00	216.83	602.49	683.65
Montane chaparral	14.07	21.08	2.46	35.48	137.71	270.40
Montane hardwood	0.00	6.86	0.00	72.12	452.08	887.27
Mt. hardwood conifer	0.00	0.00	0.00	0.00	0.00	6.44
Montane riparian	3.36	5.65	2.67	7.98	63.46	37.97
Ponderosa pine	5.34	10.77	0.00	67.20	219.52	259.73
Red fir	90.65	91.26	83.93	89.65	865.01	1534.69
Sierra mixed conifer	316.12	758.95	109.89	279.13	249.81	532.19
Wet meadow	29.11	30.32	25.84	66.44	166.58	231.69
White fir	16.65	40.30	4.87	12.07	0.00	14.46
Sparsely vegetated	0.00	0.00	0.00	0.80	13.25	42.04
Urban	0.50	1.30	0.00	3.18	3.42	3.42
Water	0.00	3.86	0.00	0.00	7.36	23.15
Total (ha)	**479.83**	**977.29**	**232.69**	**854.90**	**3417.20**	**5539.52**

varied by location (Table 5). Nonbreeding female owls preferred areas dominated by red fir and Sierra mixed conifer (e.g., Crane Flat and Big Meadow). After a large 1990 fire at Big Meadow, one nonbreeding female continued to use this area even though large portions had converted to mixed chaparral. Nonbreeding male and juvenile owls restricted their home range to primarily wet meadow, red fir, and lodgepole pine habitat types during the nonbreeding period (Table 5). A nonbreeding male that remained in the Crane Flat area throughout the year used wet meadow, Sierra mixed conifer, and red fir habitat types.

The affinity of Great Gray Owls for wet meadows becomes evident when the number of telemetry observations is examined by distance from meadows (Table 6). Over 60% (N = 3188 relocations) of all Great Gray Owl detections were within 100 m and 80% within 200 m of a meadow. Beyond 200 m the number of telemetry observations dropped dramatically, and only two owls were observed at distances greater than 1000 m from a meadow. These data become even more striking when considering that meadows comprise less than 4% of the total habitat within Yosemite National Park.

DISCUSSION

Home range size of individual Great Gray Owls that we observed in the Yosemite region of California was larger than that reported for Great Gray Owls in Canada (Nero 1980), Wyoming (Franklin 1988), and Oregon (Bull et al. 1988). Only Great Gray Owls in Europe showed larger home ranges than those that we estimated (Mikkola 1983). Great Gray Owl annual home ranges that we estimated (>2000 ha, MCP) were on average larger

Table 4. Area of vegetation cover types (ha) within adaptive kernel 75% and 95% home ranges of a breeding male Great Gray Owl during breeding and nonbreeding periods (1986–90) in Yosemite National Park, CA.

Cover Type	Breeding		Nonbreeding	
	75%	95%	75%	95%
Jeffrey pine	0.00	0.00	2.82	3.16
Lodgepole pine	0.24	0.45	1.20	1.20
Mixed chaparral	0.00	0.00	0.00	1.27
Montane chaparral	0.00	0.00	11.67	20.30
Montane hardwood	0.00	0.00	0.00	22.55
Montane riparian	0.39	0.95	7.94	18.46
Ponderosa pine	0.00	0.00	3.02	16.10
Red fir	4.80	11.15	90.20	92.26
Sierra mixed conifer	1.01	2.89	584.51	1847.06
Wet meadow	1.79	4.54	33.26	42.57
White fir	0.00	0.00	17.21	33.17
Sparsely vegetated	0.00	0.00	0.00	3.18
Urban	0.00	0.00	0.78	3.07
Water	0.00	0.00	0.00	8.52
Total (ha)	8.23	19.98	752.61	2112.87

than those estimated for Barred Owls (*Strix varia*; 231 ha, MCP), Spotted Owls (*Strix occidentalis*; 1139 ha, MCP), and Great Horned Owls (*Bubo virginianus*; 329 ha, MCP) in North America (Forsman 1980). Schoener's (1981) theory that raptor body size and home-range size are positively correlated does seem to generally hold for *Strix* owls in North America, since the largest owl, i.e., Great Gray Owls, have the largest annual home range. But, one must take into consideration that Great Gray Owls are known to be nomadic (Nero 1980). Willey and van Riper (2000) have recently demonstrated quite large home ranges in Mexican Spotted Owls in Utah, a result of postbreeding movements, much like we found for the Great Gray Owl in Yosemite.

Because AK home range estimators tend to overestimate true home range size (Worton 1989, Seaman and Powell 1996), we also used MCP estimates in all within-species and across-species comparisons. The seasonal contrast of home-range size showed that nonbreeding season transition movements (particularly during the fall) accounted for much of the variation in annual home range size among individuals during the nonbreeding period. Some owls remained close to their breeding range until heavy snows, while others moved away from the nest area early in the nonbreeding season. Given the seasonal and individual variation that we observed, multiple years of radio-tracking with a larger sample size will be required to determine realistic home ranges for successful verses unsuccessful breeding Great Gray Owls in California.

Red fir and Sierra mixed conifer were the two habitat types selected most frequently by Great Gray Owls in Yosemite. We found that Great Gray Owl home-range boundaries followed meadow and drainage topography. Bull and Henjum (1990) also demonstrated that in the Oregon, Great Gray Owl home-range size and movement generally followed

Table 5. Area of vegetation cover types (ha) within adaptive kernel 75% and 95% home ranges of nonbreeding female, male, and juvenile Great Gray Owls throughout the entire year in Yosemite National Park, CA U.S.A.

Cover Type	Nonbreeding Females		Nonbreeding Males		Juveniles	
	75%	95%	75%	95%	75%	95%
Jeffrey pine	0.41	0.41	0.00	4.90	0.00	1.74
Lodgepole pine	0.75	1.20	0.59	320.49	20.88	6.06
Montane chaparral	98.23	227.70	0.06	1.00	0.03	1.28
Montane hardwood	34.89	49.31	0.00	2.45	0.00	0.00
Montane riparian	9.16	49.31	0.43	8.67	0.64	1.52
Ponderosa pine	5.98	9.41	4.35	0.00	2.18	2.71
Red fir	10.11	29.51	17.03	230.38	25.04	105.80
Sierra mixed conifer	66.18	86.74	51.75	0.00	25.88	56.58
Wet meadow	121.32	278.30	8.83	53.59	17.46	33.52
White fir	1.79	4.54	0.86	0.00	0.43	3.14
Sparsely vegetated	0.00	0.00	0.00	0.00	0.00	0.00
Urban	0.81	1.42	0.00	0.00	0.00	0.00
Water	2.82	13.34	0.00	3.76	0.00	0.00
Total (ha)	**352.77**	**752.08**	**83.90**	**625.24**	**92.54**	**212.34**

Table 6. Number of Great Gray Owl telemetry observations ($N = 5338$) in relationship to distance in meters from meadows, divided by bird breeding status during 1986–90 in Yosemite National Park, CA U.S.A.

Bird	Distance from Meadow (m)											
Number	0	1–100	101–200	201–300	301–400	401–500	501–600	601–700	701–800	801–900	901–1000	1001+
Breeding females—breeding season												
54987	231	356	202	20	6	0	0	0	0	0	0	0
64507	264	282	105	12	0	7	9	11	2	0	0	0
54986	145	208	40	32	2	0	0	0	1	29	7	0
Subtotal	640	846	347	64	8	7	9	11	3	29	7	0
Breeding females—nonbreeding season												
54987	139	246	113	66	3	14	12	0	0	0	2	72
64507	86	178	66	0	0	25	7	4	24	0	0	0
54986	2	13	12	2	0	0	0	0	0	0	0	0
Subtotal	227	437	191	68	3	39	19	4	24	0	2	72
Breeding male –breeding season												
55000	20	33	0	0	0	0	0	0	0	0	0	0
Breeding male –nonbreeding season												
55000	138	109	29	9	2	0	5	10	0	4	17	199
Nonbreeding female												
54985	126	224	371	133	28	10	19	41	13	0	7	15
Nonbreeding males												
24209	47	72	75	31	25	12	0	0	0	0	0	0
64508	12	14	18	1	0	2	11	2	24	6	0	0
Subtotal	59	86	93	32	25	16	11	2	24	6	0	0
Juveniles												
54988-9	126	117	78	35	7	0	4	0	0	0	0	0
Totals	**1336**	**1852**	**1109**	**341**	**73**	**70**	**67**	**68**	**64**	**39**	**33**	**286**

elevation contours. This suggests that home-range size was related to features other than only elevation or the amount of forest habitat as Ganey and Balda (1989) have shown for Spotted Owls in Arizona.

We found a strong association between Great Gray Owls and meadows, regardless of home-range size and habitat type. Over 80% of owl relocations that we recorded were within 200 m of meadow sites (Table 6); i.e., the owls were relocated most often on meadow edges rather than deeper in surrounding forests. Winter (1986) reported similar results for Great Gray Owls outside Yosemite National Park, and he speculated that the isolated and patchy distribution of meadow habitat would result in nonoverlapping home ranges. As 50% of our home ranges overlapped, this suggests that habitat connectivity for the Great Gray Owl may be greater in California than originally believed. Furthermore, Bull et al. (1988) concluded that the Great Gray Owl behaves as a classic metapopulation over much of its range. In California, we believe that this might also be the case.

Finally, although the old growth red fir, Sierra mixed conifer, and lodgepole pine habitats provided areas for roosts and nesting, we believe that in California, meadow systems are the critical components of Great Gray Owl breeding and wintering habitat. It is these open areas that supply suitable hunting locations for the owl (Reid 1989). In Yosemite National Park, the nature of these meadows is confounded by the Great Gray Owl's sensitivity to human presence (Wildman 1992). Our surveys of the 16 meadow systems, where Great Gray Owls have been found historically, have shown that birds breed in only eight of the more remote meadow systems. Wildlife observations maintained by the National Park Service (NPS 2003b) indicate that breeding adults or juveniles have not been consistently seen at Crane Flat since our work in 1992. But birds do continue to breed successfully in remote meadows like McGurk (NPS 2003b). Maurer (1999) found that although there was some foraging by owls that occurred at Crane Flat in 1999, there was no evidence of nesting. He attributed the lack of breeding to the cumulative impact of visitor services development surrounding the Crane Flat meadow complex, and suggested that this has negatively influenced owl foraging behavior. This same conclusion was underscored by Wildman (1992), who found that for more than 50% of the time when owls at Crane Flat were disturbed by approaching humans, the birds did not return to the meadow to continue hunting. The continued survival of the Great Gray Owl in Yosemite may well depend not only on preservation of habitat for nesting sites, but also on understanding the importance of meadows as foraging habitat.

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