

BREEDING BIOLOGY OF THE GREAT GRAY OWL IN SOUTHEASTERN IDAHO AND NORTHWESTERN WYOMING¹

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Abstract. In this study, I documented the existence of a breeding population of Great Gray Owls (*Strix nebulosa*) in southeastern Idaho and northwestern Wyoming and recorded aspects of this species' breeding biology between 1980 and 1983. Thirty-eight pairs were found; 25 fledged young at least once. Fifteen nests were documented; 40% in old stick nests and 60% on tops of broken-top snags. Nests were frequently reused. Mean date of egg laying was 5 May. Onset of egg laying appeared to be delayed during years of higher snow depth. Mean clutch and brood sizes were 3.3 and 3.0, respectively. Seventy-one percent of the nest attempts were successful. Fledged young moved at a constant rate and direction away from the nest before they were able to fly. Northern pocket gophers (*Thomomys talpoides*) and voles (*Microtus* spp.) constituted 57.9% and 34.1% frequency of the diet, respectively. Great Gray Owls nesting near clearcuts had higher percentages of pocket gophers in their diet while those nesting near natural meadows had higher percentages of voles.

Key words: Great Gray Owl; Idaho; Wyoming; breeding biology; food habits; *Strix nebulosa*.

INTRODUCTION

The Great Gray Owl (*Strix nebulosa*) is found in the boreal climatic zones of North America and Eurasia (Mikkola 1983). The breeding range in North America is from central Alaska and Canada, south to central California, the northern Rocky Mountains, extreme northwestern Minnesota and south-central Ontario (Collins 1980, Nero 1980). Idaho and Wyoming were included in the breeding range of this species based on four records of young (Hand 1941, Johnson 1974, Collins 1980) and one nest (Craighead and Craighead 1969) observed between 1931 and 1975. In addition, 17 specimens and 12 sight records collected between 1906 and 1974 provided additional, if limited, information on the occurrence of Great Gray Owls in Idaho and Wyoming (Kemsies 1935, Bent 1938, Long 1941, Test 1941, Scott 1970, Collins 1980).

The breeding biology of Great Gray Owls has been summarized by Collins (1980) and Nero (1980) for Canada, and by Mikkola (1983) for Eurasia. However, few studies have been conducted on Great Gray Owls in the southern portion of their range in the continental United States (Winter 1979, 1981, 1982a, 1982b; Evelyn Bull, pers. comm.).

In this study, I documented a breeding pop-

ulation of Great Gray Owls in southeastern Idaho and northwestern Wyoming and recorded aspects of this species' breeding biology between 1980 and 1983.

METHODS

The study area encompassed about 24,000 km² in northwestern Wyoming and southeastern Idaho and included the Targhee National Forest (TNF), the Teton portion of the Bridger-Teton National Forest (BTNF), Grand Teton National Park (GTNP), and Yellowstone National Park (YNP) (Fig. 1). The study area was described in more detail by Franklin (1987).

Locations of Great Gray Owls within the study area were initially collected from unpublished records from the TNF, BTNF, YNP, and GTNP. Between April and August of 1980 through 1982, areas of historic observations were searched during the day for nests and surveyed during the night using broadcasted territorial calls from an 8-W cassette tape player. A limited amount of data was collected in August 1983. Surveys were used only to locate nesting pairs within the study area. The study area was not systematically censused to obtain estimates of abundance or density.

Monthly snow depths for January through May were obtained annually from 40 snow course stations (U.S. Dep. Agric. Soil Conserv. Serv.) distributed at different elevations throughout the study area.

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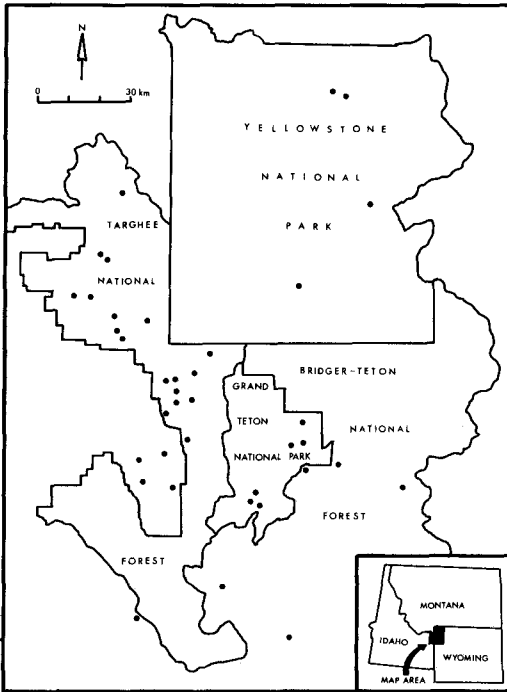


FIGURE 1. Map of the study area in southeastern Idaho and northwestern Wyoming showing locations of Great Gray Owl pairs (dots).

Time-lapse cameras were installed at three nests in 1981 and five nests in 1982 to record nesting chronology. Time-lapse cameras consisted of Minolta Autopack D6 movie cameras housed in waterproof aluminum cases. Telonics TIC-2 intervalometers were used to expose one frame of Ektachrome 160 Super 8 mm movie film every 3 min during the day. Cameras were installed above the nest in trees about 15 to 20 m from the nest. All nests were checked every 3 to 5 days by climbing trees adjacent to the nest to count eggs and young in the nests. Females usually left the nests and perched nearby during these climbs but returned to the nest within 5 min. No mortality of eggs or young was attributed to nest-site visits.

Movements from the nest and roost locations of young were documented every 3 to 5 days by searching the area surrounding the nest. At each roost location used by young, I measured the distance and direction from the nest with a compass and tape measure and the height of the young above the ground with a clinometer. Fifty-eight directions from nests to roosts of young were pooled for each nest and analyzed using circular statistics (Batschelet 1981).

Nest trees were measured after the young left the nest. At each nest tree, I measured the following variables: (1) nest height, with a clinometer, (2) diameter at breast height (DBH) of the nest tree, with a diameter tape, and (3) the surface area available for nesting, by two taped measurements across the nest surface and using the formula for computing the area of either a circle or an ellipse.

Meadow and clearcut cover-types within a 2.59-km² circle centered around nests were considered potential foraging habitat (Winter 1982a, Mikkola 1983). A 2.59-km² circle approximated the home range for Great Gray Owls (Craighead and Craighead 1969, Winter 1982a). Cover-types within the circle were outlined on aerial photographs (scale = 1:15,840) and their areas measured with a polar planimeter. Clearcuts were defined as logged areas, and meadows as natural openings. I computed a clearcut index, expressed as a percentage, by dividing the area of clearcut within the potential foraging habitat around each nest by the total area of clearcut and meadow within the potential foraging habitat.

I determined the composition of prey taken by Great Gray Owls by collecting regurgitated pellets around nests and under roost sites of young and adults. Each nest was considered a separate sampling location. Prey items were identified to species using skull characteristics (Glass 1973, Larrison and Johnson 1981). Biomass was approximated for each prey species using mean weights in Burt and Grossenheider (1964), Forsman (1975), and Weaver (1977). Skulls of northern pocket gophers (*Thomomys talpoides*) were classified as juveniles or adults based on lengths of upper and lower incisor bevels and molariform rows using criteria in Weaver (1977) and Franklin (1987). At each nest where pellets were collected, I computed a *Thomomys* index, expressed as a percentage, by dividing the frequency of *Thomomys* in the diet by the total frequency of *Thomomys* and *Microtus* in the diet.

Nonparametric tests were used for pairwise comparisons and bivariate associations (Daniel 1978, Sokal and Rohlf 1981). Tests of independence and homogeneity were evaluated using chi-square (Sokal and Rohlf 1981).

RESULTS

DISTRIBUTION AND ABUNDANCE

I recorded 255 sightings of Great Gray Owls within the study area. Most (67.5%) of the sight-

TABLE 1. Measurements of nests and nest trees of Great Gray Owls in southeastern Idaho and northwestern Wyoming. Data are $\bar{x} \pm SD$ with n in parentheses.

Nest type ^a	Height of nest aboveground (m)	DBH ^b of nest tree (cm)	Nesting surface area (cm ²)
LPP snag	4.0 ± 0.3 (3)	50.8 ± 6.7 (3)	808 ± 217 (3)
DF/ES snag	7.5 ± 1.1 (4)	71.8 ± 13.8 (4)	1,172 ± 381 (3)
All snag	6.0 ± 2.0 (7)	62.8 ± 15.3 (7)	990 ± 342 (6)
Stick	11.1 ± 2.7 (5)	38.6 ± 17.5 (5)	2,445 ± 281 (5)
Overall	8.1 ± 3.4 (12)	52.7 ± 19.9 (12)	1,651 ± 817 (11)

^a LPP = lodgepole pine, DF/ES = Douglas-fir/Engelmann spruce.

^b Diameter at breast height.

ings were from 1980 to 1983 with 94.1% occurring after 1960. Sightings were recorded between 1,524 and 3,000 m elevation. The mean elevation where active nests and fledged young were observed was 2,078 m (SD = 241, $n = 41$). Over 90% of the sightings were in the lodgepole pine (*Pinus contorta*)/Douglas-fir (*Pseudotsuga menziesii*)/aspens (*Populus tremuloides*) zone which included the lower half of the forested slopes in the area.

Thirty-eight pairs were found within the study area between 1980 and 1983 (Fig. 1). Twenty-five of the pairs were reproductively active, fledging young at least once during the 4-year study period. Twenty-four areas (defined by 2.59-km² circles) were known to be occupied by pairs for a mean of 7.2 years (SD = 8.4). One area in GTNP had been sporadically occupied between 1947 and 1983 (36 years) with young fledged in 1947 and 1981.

NEST SITES

Fifteen nests have been found in the study area; one in 1947 (Craighead and Craighead 1969), one in 1973 (D. Taylor, pers. comm.), three in 1977 (C. Youmans, pers. comm.; E. Bowman, pers. comm.), one in 1979 (T. Weaver, pers. comm.), and nine during this study.

Nine (60%) of the nests were in shallow depressions on the tops of broken-top snags. Five of these were in lodgepole pine snags, three in Douglas-fir snags and one in an Engelmann spruce (*Picea engelmannii*) snag. All of the snags were in advanced stages of decay (sensu Cline et al. 1980). Six (40%) of the nests were in old stick nests; four were in lodgepole pines, one in an aspen, and one in a Douglas-fir snag.

Nests in lodgepole pine snags were lower to the ground and had the smallest surface area (Table 1). Stick nests were the highest and had the largest surface area. Nests in snags (all tree species combined) were significantly closer to the ground

(Mann-Whitney U -test, $U = 33$, $P < 0.05$), in trees of larger DBH ($U = 30$, $P < 0.05$), and had smaller surface areas ($U = 30$, $P < 0.01$) than stick nests.

Nest destruction over 2 years appeared greatest in lodgepole pine snags followed by stick nests. Two lodgepole pine snags used for nesting were felled during a windstorm while a third was depredated. Two stick nests were destroyed by wind. I observed no loss of nests in Douglas-fir/Engelmann spruce snags.

Five nests observed over a 2-year period (one nest in 1947–1948, F. Craighead, pers. comm.; two nests in 1977–1978, C. Youmans, pers. comm.; two nests in 1981–1982, this study) were occupied each year and were reproductively successful. A sixth nest was used for four consecutive years (1980 to 1984), producing two to three young each year. A seventh nest was active in 1980, 1981, and 1983, but not in 1982. In 1982, time-lapse films recorded an adult on this nest

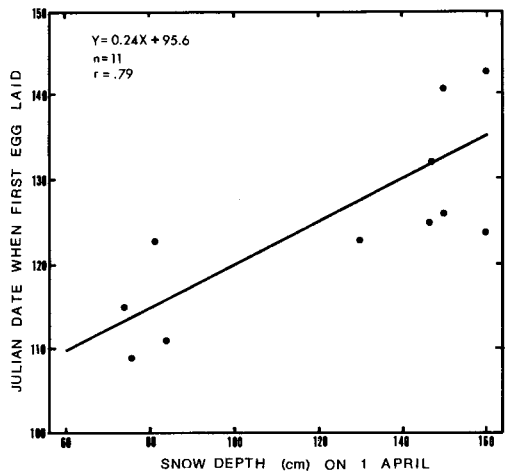


FIGURE 2. Julian date of first egg laid in relation to snow depth on 1 April at Great Gray Owl nests in southeastern Idaho and northwestern Wyoming. Spearman's rank correlation coefficient is significant at $P < 0.01$.

TABLE 2. Reproductive output of Great Gray Owls in southeastern Idaho and northwestern Wyoming.

	Observed frequency of <i>n</i> ^a individuals				\bar{x}	SD	<i>n</i>
	1	2	3	4			
Clutch size	0	2	2	4	3.3	0.3	8
Brood size	1	2	6	4	3.0	0.3	13
Size of fledgling groups ^b	1	0	4	2	3.0	0.4	7
Size of fledgling groups able to fly	1	3	1	0	2.0	0.3	5

^a *n* = number of eggs for clutch size and number of young for the other three variables.

^b Not yet capable of flight.

for 15 to 20 min on 27 April and 1 May with no other activity recorded for the rest of the year.

NESTING CHRONOLOGY

Before egg laying, adults were frequently recorded at the nest. Time-lapse photography at two nests revealed that adults repeatedly visited the nests 17 to 25 days before the females settled on the nest. One or both of the owls made at least one to four trips daily to the nest ($\bar{x} = 2.3$, SD = 1.0, *n* = 19) each or every other day and spent 3 to 75 min at the nest ($\bar{x} = 15$, SD = 16, *n* = 42) during daylight visits.

The mean date when the first egg was laid was 5 May (SD = 9.9 days, *n* = 11). The date when the first egg was laid was significantly correlated with snow depth at the onset of the breeding season (defined as 1 April) (Fig. 2). Eggs were laid as early as 19 April under conditions of relatively shallow snow and as late as 23 May when snow was deeper.

Incubation period (from the laying of the first egg to the hatching of the last egg) averaged 29.7 days (SD = 1.6, *n* = 3 clutches). Young left their nests at a mean age of 28.5 days (SD = 1.5, *n* = 6). At this stage, the young were considered fledged even though they were incapable of flight. Young were capable of sustained gliding flight an average of 14.2 days (SD = 1.1, *n* = 5) after leaving the nest.

REPRODUCTIVE OUTPUT

The most common clutch was three to four eggs (75.0%) and the most common brood was three to four young (76.9%) (Table 2). Annual clutch size ranged from a mean of 3.0 (*n* = 4) in 1981 to 3.3 (*n* = 4) in 1982. Clutch sizes in this study were not statistically different (Mann-Whitney *U*-test, *U* = 110–149, *P* > 0.50) from clutch sizes from two other studies in North America (Oeming 1955 [*n* = 23 clutches], Collins 1980 [*n* = 11]). However, comparison of the pooled data from North America with data from four studies

(*n* = 21, 28, 30, and 66 clutches) in Finland and Sweden (Hildén and Helo 1981), which also were not significantly different (Mann-Whitney *U*-test, *U* = 380–898, *P* > 0.12), revealed that clutch sizes in North America ($\bar{x} = 3.2$, *n* = 34) were significantly smaller (Mann-Whitney *U*-test, *U* = 3,709, *P* < 0.001) than clutch sizes in Scandinavia ($\bar{x} = 4.3$, *n* = 145).

Between 1980 and 1983, eggs were laid in 88.2% of 17 nesting attempts while young were fledged in 70.5% of the attempts. Nests in lodgepole pine snags, stick nests and fir/spruce snags averaged 1.0 (*n* = 4), 3.0 (*n* = 4), and 3.3 (*n* = 4) fledglings per nesting attempt, respectively. The annual number of fledglings per successful nest, or productivity, ranged from a mean of 2.7 (*n* = 3) in 1981 to 3.0 (*n* = 3) in 1982.

Survival probabilities for young were determined at eight nests where eggs and young were followed through most or all of the developmental stages. A young Great Gray Owl had a probability of 0.76 (*n* = 25) of surviving incubation as an egg, 0.89 of surviving as a nestling (*n* = 19), and 0.77 of surviving through the flightless stage after fledging (*n* = 13).

MOVEMENTS OF FLEDGLINGS

Eleven banded young, fledged from five nests, moved at a constant rate (Fig. 3) and in a constant direction (*n* = 58 directions measured) away from the nest as they grew older. Mean directions taken by family groups were roughly north (*n* = 2; 19° and 32°), south (*n* = 1; 176°), and southwest (*n* = 2; 224° and 250°). The *r* values for the mean directions were high (range = 0.83–0.96) and significantly directed (Rayleigh test, *P* < 0.001) indicating that each family group maintained a constant compass direction as they moved away from the nest.

The height which fledglings roosted above the ground was significantly correlated with the age of the fledglings (Fig. 4). The roost sites used by fledglings as they moved away from their nests,

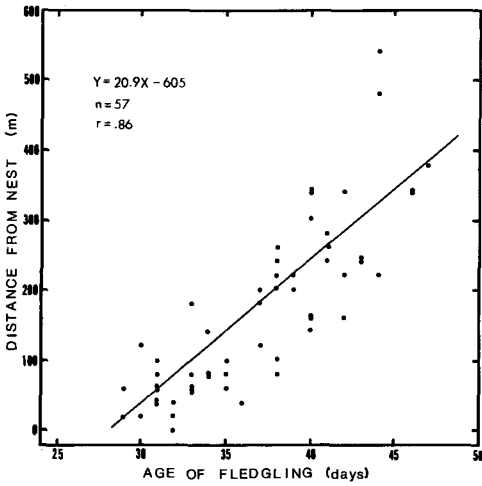


FIGURE 3. Distances moved from nests by fledgling Great Gray Owls in relation to their age in southeastern Idaho and northwestern Wyoming. Spearman's rank correlation coefficient is significant at $P < 0.001$.

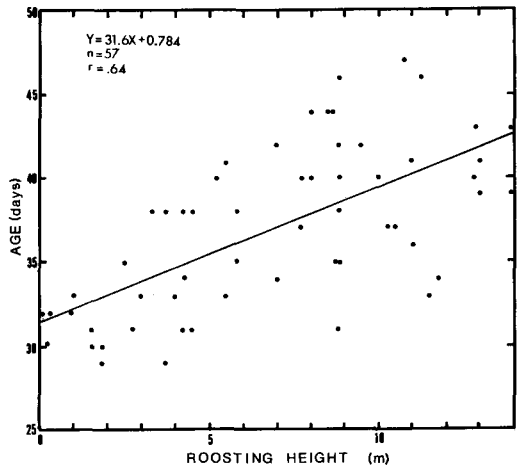


FIGURE 4. Height at which fledgling Great Gray Owls roosted in relation to their age in southeastern Idaho and northwestern Wyoming. Spearman's rank correlation coefficient is significant at $P < 0.001$.

but before they could fly, were assigned to three categories (Fig. 5); (1) most accessible to the young ($n = 8$), (2) moderately accessible ($n = 18$), and (3) least accessible ($n = 31$). Mean age of young using the three categories of roosts differed significantly (Mann-Whitney U -test, $U = 112-433$, $P < 0.05$). Accessibility was subjectively determined by the ease with which roosts could be reached by fledglings that could not fly. Vulnerability to mammalian predators was considered a direct function of accessibility.

FOOD HABITS

Northern pocket gophers and *Microtus* spp. constituted 92.0% (by frequency) and 92.9% (by biomass) of 435 prey items identified from pellets collected at eight nests (Table 3). Of 72 pocket gopher skulls aged, 76.4% were from juveniles; 65.8% from pellets collected in June ($n = 38$), 90.9% in July ($n = 22$), and 87.8% in August ($n = 8$).

Comparisons of the frequency of prey items placed in three categories (*Thomomys*, *Microtus*, and "Other" prey) resulted in three nest groups, containing nests not significantly different from each other. Nest group A ($\chi^2 = 13.0$, $df = 8$, $P > 0.10$) included five nests ($n = 199$ prey items) which fledged a mean of 2.9 young ($SD = 1.1$, $n = 7$), group B ($\chi^2 = 4.8$, $df = 2$, $P > 0.05$) included two nests ($n = 72$ prey) which fledged an average of 3.0 young ($n = 2$), and group C ($\chi^2 = 4.1$, $df = 2$, $P > 0.05$) included two nests ($n = 160$ prey)

where the reproductive outcome was unknown. Differences in frequencies of *Thomomys* and *Microtus* among all three nest groups were significant ($\chi^2 = 4.3-92.3$, $df = 1$, $P < 0.05$) but not significant in the Other category ($\chi^2 = 0.1-1.2$, $df = 1$, $P > 0.25$). Percentages of *Thomomys* in the diet decreased, as *Microtus* increased, in groups A, B, and C, respectively (Fig. 6).

The differences in occurrence of prey may be partially explained by the types of foraging habitat around the nests. The amount of *Thomomys* in the diet appeared directly proportional to the amount of clearcut surrounding the nests (Fig. 7).

DISCUSSION

Productivity in this study was high with a mean of 3.0 young fledged per successful nest as com-

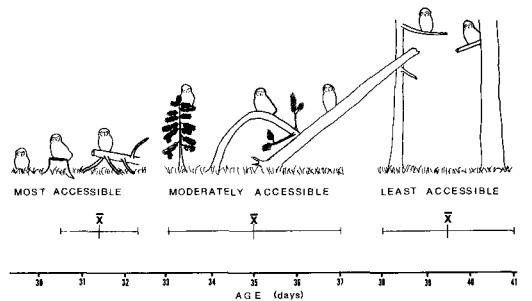


FIGURE 5. Mean age of fledgling Great Gray Owls using three categories of roosts in southeastern Idaho and northwestern Wyoming. Values represent means \pm 95% confidence intervals around the mean.

TABLE 3. Prey items found in Great Gray Owl pellets in southeastern Idaho and northwestern Wyoming.

Prey species	n	Frequency (%)	Biomass (g)	Biomass (%)
<i>Thomomys talpoides</i>	252	57.9	17,415	69.4
<i>Microtus montanus</i>	139	32.0	5,560	22.1
<i>Microtus agrestis</i>	2	0.5	80	0.3
<i>Microtus richardsoni</i>	7	1.6	280	1.1
<i>Peromyscus maniculatus</i>	7	1.6	154	0.6
<i>Sorex</i> spp.	6	1.4	60	0.2
<i>Tamiasciurus hudsonicus</i>	3	0.7	600	2.4
<i>Clethrionomys gapperi</i>	3	0.7	75	0.3
<i>Zapus princeps</i>	3	0.7	90	0.4
<i>Onychomys leucogaster</i>	3	0.7	90	0.4
Unidentified bird	10	2.2	700	2.8
Total	435	100.0	25,104	100.0

pared to 2.3 in Oregon (Evelyn Bull, pers. comm.) and 2.7 to 3.9 in Finland and Sweden (Hildén and Helo 1981). Nesting success in this study was also high and similar to that observed in Oregon (75%, Evelyn Bull, pers. comm.). Despite larger clutches in Finland, the average number of fledglings per nest attempt ($\bar{x} = 2.4, n = 42$) in Finland (Mikkola 1981) was similar to that found in this study because of lower nestling survival in Finland than in this study (72% vs. 89%, respectively). Hatching rates were similar (81% in Finland and 76% in this study).

In this study, nests in fir/spruce snags were more productive and stable than nests in lodgepole pine snags and stick nests. Those in fir/spruce snags (1) had a larger nesting surface area, (2) were taller and, therefore, relatively inaccessible to predators, and (3) were more durable.

Great Gray Owls in North America use different proportions of stick nests and broken-top snags for nesting within different parts of their geographic range. In order of decreasing latitude, the ratio of snag to stick nests average 1:20 ($n = 42$) in Canada and Minnesota (Roberts 1936; Robinson 1954; Oeming 1955; Parmelee 1968; Nero 1970, 1984; Muir 1972; Kondla 1973; James 1977; Eckert 1979; Collins 1980; Houston and Wylie 1984), 1:2.5 ($n = 41$) in Oregon (Evelyn Bull, pers. comm.), 1:0.7 ($n = 15$) in this

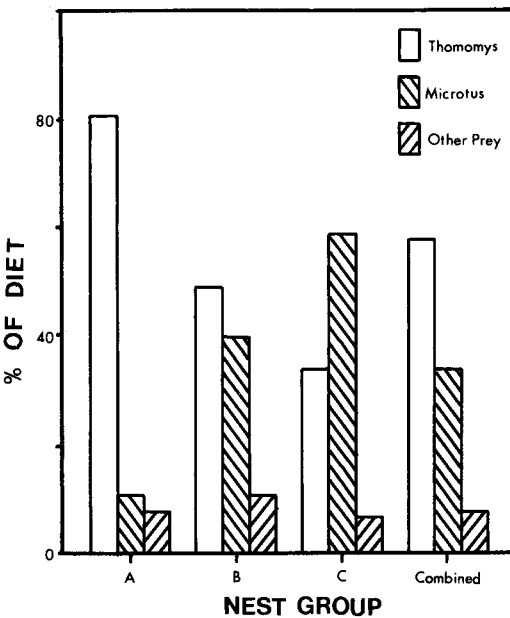


FIGURE 6. Percent of three prey categories in three groups of Great Gray Owl nests in southeastern Idaho and northwestern Wyoming. Prey categories and nest groups are explained in the text.

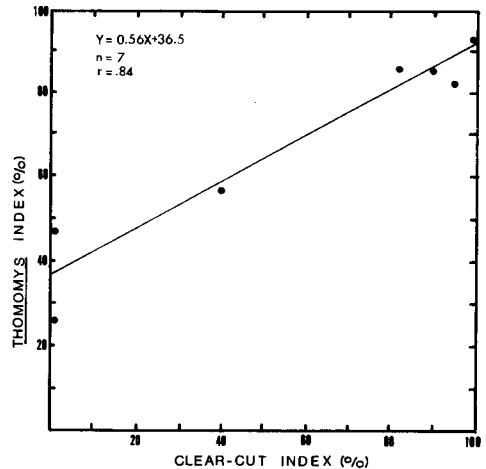


FIGURE 7. *Thomomys* index in relation to clearcut index at seven nests in southeastern Idaho and northwestern Wyoming. Spearman's rank correlation coefficient is significant at $P < 0.03$.

study and 1:0 ($n = 8$) in California (Winter 1980, 1982a). Use of snags for nests is almost three times more common in southern than in central and northern Finland (Mikkola 1983). The use of snags as nests may be related to nest-site availability within different proportions of this species' breeding range.

After leaving the nest, young climbed available perches near the nest probably to escape ground predators (Oeming 1955; Høglund and Langsgren 1968; Nero 1970, 1984; Pulliainen and Loisa 1977; Follen 1979; Collins 1980). Survival of fledged young probably depends on: (1) the availability of roosts such as leaning and deformed trees which are accessible to them and which allows them to roost high enough to avoid ground predators and (2) the existence of forested habitat within a 500-m radius surrounding the nest. The reason for the unidirectional movements by family groups is unknown and appears to be unpredictable. However, Nero (1980) observed a female using vocalizations to lure young away from the nest indicating that movements by young may be controlled by their parents.

During the breeding season, over 90% of the prey in Great Gray Owl diets in Europe and Canada was in the family Microtidae (Oeming 1955; Høglund and Langsgren 1968; Nero 1969; Mikkola and Sulkava 1970; Mikkola 1972, 1981; Pulliainen and Loisa 1977). However, pocket gophers (*Thomomys* spp.) constituted 34 to 58% of the diet of Great Gray Owls in the southern part of their range in North America (Evelyn Bull, pers. comm.; Winter 1982a; this study). Therefore, pocket gophers appear to be an important prey for Great Gray Owls in the southern portion of their North American range.

In this study, Great Gray Owls nesting near clearcuts may be utilizing the most abundant small mammal species available. Barnes (1973) and Teipner et al. (1983) reported higher densities of pocket gophers in clearcut areas than in other habitats. In addition, juvenile pocket gophers were present in the diet in higher percentages than were typically present in the age structure of northern pocket gopher populations. The proportion of juvenile gophers found in YNP by Youmans (1979) was 7% in June, 39% in July, and 78% in August as compared to 66%, 91%, and 88% juvenile gophers in the diet of Great Gray Owls in this study during those months, respectively. Great Gray Owls may be taking the most vulnerable age class of this prey since young

pocket gophers often disperse aboveground (Chase et al. 1982). Winter (1982a) suggested that reduced microtine abundance could severely limit reproduction by Great Gray Owls. In this study, however, fledgling success was high at nests where high percentages of pocket gophers were present in the diet.

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