

## FOREST STRUCTURE AND PREY ABUNDANCE IN FORAGING AREAS OF NORTHERN GOSHAWKS

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**Abstract.** The U.S. Forest Service recently recommended managing forests to increase the abundance of prey for Northern Goshawks (*Accipiter gentilis*) in the southwestern United States. However, empirical data are needed to indicate whether goshawks select foraging habitat based on prey abundance, on the presence of forest structures that favor their hunting strategy, or both. During the 1993 and 1994 breeding seasons, we indexed prey abundance and measured forest structure at sites used by radio-tagged goshawks and at nearby paired sites that lacked evidence of goshawk use (contrast plots). Goshawks apparently did not select foraging sites based on prey abundance; indeed, abundances of some prey were lower on used than on contrast plots. Goshawks selected foraging sites that had higher canopy closure ( $P = 0.006$ ), greater tree density ( $P = 0.001$ ), and greater density of trees  $>40.6$  cm dbh ( $P < 0.0005$ ) than on contrast plots. These results are consistent with the hypothesis that goshawk morphology and behavior are adapted for hunting in moderately dense, mature forests, and that prey availability (as determined by the occurrence of favorable vegetation structure where prey are present above a low threshold) is more important than prey density in habitat selection. Nonetheless, current management recommendations for increasing prey abundance also can create a forest structure more favorable for hunting by goshawks, particularly if stands are managed for canopy closure values above the prescribed minimum level of 40% canopy.

**Key words:** *Accipiter gentilis*; Arizona; foraging; forest structure; habitat selection; Northern Goshawk; ponderosa pine forest; prey abundance; prey availability; raptors.

### INTRODUCTION

Since 1982, when the U.S. Forest Service listed the Northern Goshawk (*Accipiter gentilis*) as a sensitive species in the southwestern United States, nest stands ( $\geq 8$  ha) have been protected from timber harvest (Reynolds 1983). Despite this protection, Crocker-Bedford (1990) found that goshawk reproduction in southwestern forests declined following timber harvesting in adjacent areas, perhaps because logging gave a competitive advantage to open-forest raptors, made hunting more difficult, or decreased the abundance of prey. In response, Reynolds et al. (1992) recommended managing these forests for abundant populations of the 14 species that are the goshawk's primary prey. However, the Arizona Game and Fish Department (1993) and the U.S. Fish and Wildlife Service (Spear 1993) argued that, because accipiter hawks are adapted to forage in forested habitats, prey availability (as determined by forest structure) is more crucial than prey abundance.

Although many studies (summarized by Reynolds et al. 1992) have shown that goshawks prefer forest stands with large trees and high canopy closure for nesting, only five studies have compared available habitat to the habitats that goshawks use for activities other than nesting, and none of these studies measured prey abun-

dance. The three North American studies found that goshawks used all forest types, but preferred stands with average tree diameter  $\geq 52$  cm dbh (diameter breast height; Austin 1993), greater canopy cover, basal area, and tree densities (Hargis et al. 1994), and areas with high canopy closure, as determined from LANDSAT imagery (Bright-Smith and Mannan 1994). The two European studies found that goshawks spent 50% of their time and took 70% of their prey in woodland that comprised only 12% of their habitat amid farmland in England (Kenward 1982); they preferred edge zones in areas with 41–61% woodland amid Swedish farmland (Kenward 1982); and they preferred mature conifers over younger stands in Swedish boreal forest (Widén 1989).

Studies of habitat selection, depending on their objectives, can focus on different scales of selection. The analysis of differences between home ranges and the habitat available in the region (e.g., Hargis et al. 1994) has been termed macrohabitat selection (Ratti and Garton 1994:16) or second-order habitat selection (Johnson 1980). The analysis of differences between used sites and habitat available within the home range (e.g., Kenward 1982, Bright-Smith and Mannan 1994) illustrates microhabitat (Ratti and Garton 1994), or third-order selection (Johnson 1980). Independently of the scale of selection, habitat descriptions can be general (when a site is categorized into one of several broad vegetation types, e.g., Austin 1993, Bright-Smith and

Mannan 1994), or detailed (when habitat characteristics are measured at specific sites, e.g., Hargis et al. 1994). Because goshawk prey (birds and small mammals) vary in abundance over small spatial and temporal scales, both within a goshawk home range and within a vegetation type, the microhabitat scale and more detailed resolution are appropriate for assessing the role of prey abundance in habitat selection.

We radio-tracked goshawks and compared prey abundance and vegetation structure at sites used by active (presumably hunting) goshawks with nearby plots that lacked evidence of goshawk use. Our objective was to address the importance of vegetation structure and prey abundance in microhabitat selection during the breeding season, for goshawks nesting in ponderosa pine (*Pinus ponderosa*) forests.

## METHODS

### Study area

The study area included the Coconino National Forest and nearby portions of the Kaibab National Forest, northern Arizona. Elevations of areas used by goshawks ranged from  $\approx 2000$  to 2600 m, with gentle topography over most of the plateau. The climate was cool, with an early summer drought. During 1964–1993, Flagstaff (elevation 2125 m) had a mean annual precipitation of 54 cm (including 196 cm of snowfall during December to March) and mean annual temperature of 7.6°C. Average daily low and high temperatures were  $-10^\circ$  and  $5^\circ\text{C}$  in January, and  $10^\circ$  and  $28^\circ\text{C}$  in July (National Oceanic and Atmospheric Administration 1993).

The forest was dominated by ponderosa pine (*Pinus ponderosa*). At lower elevations, pinyon pine (*P. edulis*), alligator juniper (*Juniperus deppeana*), Utah juniper (*J. osteosperma*), and Gambel oak (*Quercus gambelli*) were common understory trees. At higher elevations and on north-facing slopes, limber pine (*P. flexilis*) and Douglas-fir (*Pseudotsuga menziesii*) were co-dominant with ponderosa pine, and aspen (*Populus tremuloides*) occurred in the understory or in small, pure stands. Except in areas of dense pine or oak seedlings, understories were generally open. Common understory species included lupine (*Lupinus* spp.), New Mexican locust (*Robinia neomexicana*), Arizona rose (*Rosa arizonica*), buckbrush (*Ceanothus fendleri*), snakeweed (*Gutierrezia* spp.), Oregon grape (*Berberis repens*), showy aster (*Aster commutatus*), and grasses such as Arizona fescue (*Festuca arizonica*), mountain muhly (*Muhlenbergia montana*), and mutton bluegrass (*Poa fendleriana*). Plant names follow Kearney and Peebles (1964).

### Radio-tracking

We captured 20 adult ( $\geq 2$ -yr-old) goshawks at nest sites during 1992–1994. We attached a radio transmitter to each bird with a backpack harness made from 6 mm

wide tubular teflon ribbon. Most transmitters contained tipswitches that caused a slow pulse rate in vertical orientation (typical of a perching bird) and a faster pulse rate in a horizontal position (typical of flight). Tipswitch packages averaged 22 g, or  $\approx 3.3\%$  and  $2.2\%$  of the average body mass of males and females, respectively; each of the five transmitters without tipswitches had a mass of  $\approx 18$  g.

During 8 July to 25 September 1993 and 18 May to 25 August 1994, teams of two people tracked individual birds for periods of 1–9 h to locate foraging birds  $>200$  m away from their nests. Using the flight and perch durations reported by Kenward (1982), Widén (1984), and Kennedy (1990), we presumed that the focal goshawk was foraging when periods of fast pulse rate  $<3$  min in duration alternated with periods of slow pulse rate  $<12$  min in duration. To minimize disturbance, trackers stayed together until they were  $<200$  m from an apparently foraging bird. Then the observers split up, maintaining two-way radio contact, until their azimuths formed a  $60$ – $120^\circ$  angle and signal volume suggested that they were each  $\approx 100$ – $150$  m from the goshawk. Then the observers quietly followed their azimuths, pacing their distance until they met. Either the observed goshawk location or the intersection of the two azimuth lines was flagged as the center of a used plot. If the paced length of an azimuth line exceeded 150 m and we did not see the goshawk flush, we did not use the point as a plot center and we left that bird for  $>4$  h. Because goshawks often flew while the observers were trying to move into an optimum angular configuration, most walk-in attempts failed. On average,  $\approx 10$  h (including failed attempts) were required for a two-person crew to obtain a location.

To estimate location error, in December 1995, two crews (each with one experienced and one inexperienced technician) located 23 transmitters attached to saline bottles positioned  $<2$  m above the ground. When signal strength and quality suggested that the transmitter was  $\approx 100$  m away, observers turned off their telemetry receivers and paced out their azimuths. We found a mean error of  $22 \pm 15$  m (mean  $\pm 1$  SD); the three largest errors were 37, 50, and 62 m. This may overestimate our actual error because goshawk locations were determined by experienced field crews, goshawks often perched at heights  $>2$  m (soil near the transmitter antenna attenuates and alters the polarity of the radio signal; Cochran 1980), and observers walking in on goshawks usually took final azimuths at distances well under 100 m.

Only these precise walk-in locations were used as centers of used plots. For each used plot, we located a paired contrast plot in a random direction  $>500$  m from the walk-in location; we further stipulated that the paired contrast plot be  $>200$  m from any previous radio location (including less precise locations obtained from weekly airplane flights and from ground locations at distances  $>150$  m from the goshawk). To avoid gos-

hawk locations, the centers of some contrast plots were up to 1000 m from the paired used plot, but always within the minimum convex polygon home range (Mohr 1947); at least 30 locations, each obtained  $\geq 6$  h apart, were used to define each home range. We chose a 500-m offset because 8-h monitoring sessions of goshawks in 1992 showed that individuals tended to use several activity areas, each with a radius of  $\approx 300$  m (P. Beier, unpublished data). This paired sampling strategy has more statistical power than strict random sampling (Ratti and Garton 1994:15–16).

#### Prey abundance

We indexed prey abundance on each used plot and its paired contrast plot on the same day, usually 1 d (maximum 4 d) after the goshawk location was obtained. Thus, we attempted to sample the same prey population that was available to the goshawk. We indexed abundance of avian prey for a 10-min period  $< 1$  h after sunrise, and a second 10-min period  $< 2$  h before sunset, counting all birds heard or seen within 50 m of the plot center; birds detected at greater distance were recorded, but excluded from the analyses (Ralph et al. 1993). We grouped avian prey into three classes for analysis, using body masses reported in Terres (1991). Large birds (75–145 g) included American Robin (*Turdus migratorius*), Steller's Jay (*Cyanocitta stelleri*), Northern Flicker (*Colaptes auratus*), Lewis' Woodpecker (*Melanerpes lewis*), Mourning Dove (*Zenaidura macroura*), and Clark's Nutcracker (*Nucifraga columbiana*). Medium birds (30–62 g) included Hairy Woodpecker (*Picoides villosus*), Hermit Thrush (*Catharus guttatus*), bluebirds (*Sialia* spp.), and Evening Grosbeak (*Coccothraustes vespertinus*); small birds (12–21 g) included House Finch (*Carpodacus mexicanus*), Pine Siskin (*Spinus pinus*), nuthatches (*Sitta* spp.), Dark-eyed Junco (*Junco hyemalis*), and most flycatchers (Tyrannidae). Blue Grouse (*Dendragapus obscurus*) were not present in goshawk home ranges.

We indexed the abundance of diurnal mammals by the number of track stations visited by each mammal species, for 100 track stations (J. E. Drennan and P. Beier, unpublished manuscript) placed on a 10-  $\times$  10-trap grid with 15-m spacing (i.e., 2.25 ha). We set out stations immediately after the dawn counts for avian prey, and retrieved them 1 h before sunset, at which time we recorded all animal tracks to genus. J. E. Drennan and P. Beier (unpublished manuscript) found that the number of track stations visited was highly correlated with numbers of diurnal squirrels subsequently trapped. For analysis, we grouped squirrels by size into three groups: Abert's and rock squirrels (*Sciurus aberti* and *Spermophilus variegatus*), red squirrels and mantled ground squirrels (*Tamiasciurus hudsonicus* and *Spermophilus lateralis*), and grey-collared and cliff chipmunks (*Eutamias cinereicollis* and *E. dorsalis*). Boal and Mannan (1994) reported that these species, as well as cottontail rabbits (*Sylvilagus* spp.), were im-

portant prey for goshawks on the nearby Kaibab Plateau. On our study area, however, red squirrels were present in only one goshawk home range, and cottontails were rarely detected on our track stations. We believe that this reflects low cottontail numbers (not a failure of our sampling effort), because we saw cottontails on only four occasions during this study and, in each case, our track stations detected cottontails on the plots. Cottontails are usually rare in the ponderosa pine forests of Arizona (Hoffmeister 1986).

#### Forest structure

We characterized forest structure on 75 m radius (1.77-ha) plots, using the same plot centers as on the prey surveys. We sampled along one 150 m diameter line (0°) and the outer 70 m of four radii (60°, 120°, 240°, 300°). This gave greater weight to vegetation near the plot center (the goshawk location on used plots), but avoided resampling vegetation at the plot center. We chose this plot size because Kenward (1982) reported that 95% of goshawk attacks were made directly from perches and that attack distances (perch to prey) averaged 54 m in woodlands and 103 m in more open country. We used Biltmore sticks and diameter tapes to measure diameters of all trees within 1 m of each radius. We collapsed tree diameter data into three classes before analysis. We measured both canopy closure and ground cover by point intercept at 91 points (plot center and every 5 m along each radius); vertical sighting tubes insured that canopy closure was measured directly overhead. We counted the numbers of shrubs and saplings intercepted by the diameter and radial segments. On 14% of the plot, we tallied all large ( $\geq 30.5$  cm dbh) and small snags, and all large ( $\geq 30.5$  cm in diameter at midpoint and  $\geq 2.4$  m long) and small logs (15.2–30.5 cm in diameter at midpoint and  $> 1.2$  m long, or  $\geq 30.5$  cm in diameter and 1.2–2.4 m long). We also recorded percent slope, aspect (to the nearest multiple of 45°), and topographic position (flat, mid-slope, ridge, or drainage bottom).

#### Data analysis

We examined frequency distributions and used compositional analysis (Aebischer et al. 1993) to test for differences between used and contrast plots in aspect, topographic position, and percent ground cover. For all other variables, we computed the difference in prey abundance indices and vegetation parameters between each used plot and its paired contrast plot, and then averaged these differences separately for each goshawk for which we sampled at least two pairs of plots. Using the bird as the sampling unit, we used *t* tests to test whether or not the mean difference across birds differed from zero. Before statistical analyses, we applied a square-root transformation to all counts and an arcsine square-root transformation to canopy closure percentages.

TABLE 1. Abundance of prey on 56 plots used by adult Northern Goshawks in northern Arizona, May–September 1993–1994, and on 56 paired contrast plots, averaged across 14 adult goshawks (nine females, five males) with at least two pairs of plots per goshawk. Mammal abundance was indexed by the number of track stations visited on a 2.25-ha plot, and (except as noted for large birds) bird abundance was indexed by counts on 50-m radius plots.

| Prey group                                 | Used plots |      | Contrast plots |      | Difference, used – contrast |       | P† |
|--------------------------------------------|------------|------|----------------|------|-----------------------------|-------|----|
|                                            | Mean       | 1 SD | Mean           | 1 SD |                             |       |    |
| Abert's and rock squirrels                 | 0.82       | 2.1  | 0.60           | 1.1  | +0.22                       | 0.91  |    |
| Mantled ground squirrels and red squirrels | 2.14       | 2.0  | 3.49           | 3.6  | -1.35                       | 0.20  |    |
| Chipmunks                                  | 2.92       | 2.8  | 2.49           | 1.8  | +0.44                       | 0.84  |    |
| Large birds                                | 0.84       | 0.9  | 0.77           | 0.8  | +0.07                       | 0.62  |    |
| Large birds (unbounded plot)               | 2.91       | 1.6  | 2.72           | 1.8  | +0.19                       | 0.09  |    |
| Medium birds                               | 1.01       | 0.8  | 2.30           | 2.1  | -1.29                       | 0.006 |    |
| Small birds                                | 6.85       | 3.5  | 8.63           | 3.1  | -1.78                       | 0.06  |    |

† Two-tailed, paired-sample *t* test (df = 13) of the null hypothesis that the mean difference is zero.

RESULTS

We sampled vegetation on two pairs of plots for each of four goshawks, on three pairs of plots for one goshawk, and on 4–7 pairs of plots for each of 11 goshawks. Thus, we sampled vegetation on at least two pairs of plots for each of 10 female and six male goshawks (a total of 63 pairs of plots). Because seven of these pairs were not sampled for prey abundance, we indexed prey abundance at two or more pairs of plots for each of nine female and five male goshawks. We

observed a radio-tagged goshawk perched or flushing (*n* = 38 cases), or found only prey remains (*n* = 7) or goshawk feathers (*n* = 2) at the center of 70% of the used plots.

Contrary to our expectations, prey were not more abundant on used plots than on contrast plots. Indeed, medium-sized birds were significantly less abundant on used plots (Table 1, Fig. 1). We detected no Abert's and rock squirrels on 86 of 112 plots, contributing to mean differences of zero in this prey category for eight of the 14 goshawks. Similarly, we detected, on average, only 0.8 large avian prey on each 50-m plot, and the low density of these birds relative to our sampling effort made it difficult to detect differences. Therefore we reanalyzed our data for large birds to include large birds detected beyond 50 m. Data for the unbounded plots showed a slightly larger, statistically nonsignificant, difference (Table 1).

Used plots surpassed contrast plots in canopy closure, tree density, and density of the largest trees (Table 2, Figs. 2 and 3). Canopy closure was 5% greater on used plots vs. contrast plots, and the difference was consistent across birds (Fig. 2). There were no differences between used and contrast plots in percent slope, aspect, or topographic position.

To further investigate the canopy closure and tree density differences, we examined their correlation with two variables related to understory vegetation. Across all 134 plots, percent grass–forb ground cover declined steeply with increasing canopy closure (*r* = -0.38, *P* < 0.0005) and increasing tree density (*r* = -0.39, *P* < 0.0005), but the number of shrubs intercepting 430 m of tape was poorly correlated with canopy closure (*r* = -0.14, *P* = 0.11) and tree density (*r* = -0.18, *P* = 0.04). Despite these correlations and the significant differences in overstory variables, used and contrast plots did not differ in grass–forb cover or shrub–sapling numbers (Table 2). Across all plots, the understory was uniformly open: only 13% of 134 plots had <50% litter

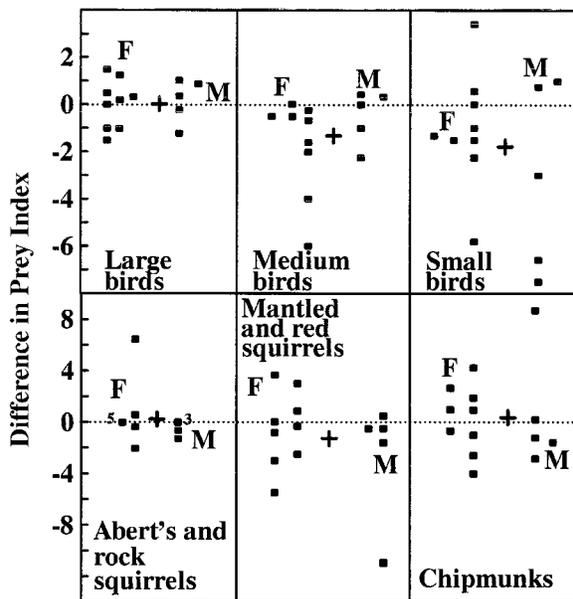


FIG. 1. Differences in prey abundance between plots used by adult goshawks in northern Arizona during May–September 1993–1994, and paired contrast plots. Each rectangle indicates the mean difference (used – contrast) for one adult female (left, *n* = 9) or one adult male (right, *n* = 5), each with at least two pairs of plots per goshawk; “+” represents the grand mean across 14 goshawks. Numbers in the graph for Abert's and rock squirrels indicate the number of birds with a mean difference of zero.

TABLE 2. Vegetation and physical characteristics on 63 1.77-ha plots used by adult goshawks in northern Arizona during May–September 1993–1994, and on 63 paired contrast plots, averaged across 16 adult goshawks (10 females, six males) with at least two pairs of plots per goshawk.

| Characteristic                                       | Used plots |      | Contrast plots |      | Difference,<br>used – contrast | <i>P</i> |
|------------------------------------------------------|------------|------|----------------|------|--------------------------------|----------|
|                                                      | Mean       | 1 SD | Mean           | 1 SD |                                |          |
| Aspect (% of plots)                                  |            |      |                |      |                                | 0.60†    |
| N and NE                                             | 31         | 28   | 26             | 23   |                                |          |
| E and SE                                             | 13         | 18   | 18             | 23   |                                |          |
| S and SW                                             | 20         | 26   | 18             | 23   |                                |          |
| W and NW                                             | 18         | 27   | 10             | 13   |                                |          |
| Flat                                                 | 16         | 21   | 26             | 33   |                                |          |
| Topographic position (% of plots)                    |            |      |                |      |                                | 0.69†    |
| Ridgetop                                             | 6          | 14   | 4              | 9    |                                |          |
| Midslope                                             | 59         | 35   | 55             | 32   |                                |          |
| Canyon bottom                                        | 8          | 16   | 6              | 14   |                                |          |
| Flat                                                 | 26         | 32   | 33             | 33   |                                |          |
| Ground cover (%)                                     |            |      |                |      |                                | 0.18†    |
| Grasses and forbs                                    | 9.7        | 8.7  | 9.9            | 8.0  | –0.2                           |          |
| Bare ground, including roads                         | 12.2       | 5.1  | 14.7           | 6.1  | –2.4                           |          |
| Litter                                               | 68.5       | 12.0 | 66.1           | 10.0 | +2.5                           |          |
| Downed wood or stump                                 | 3.1        | 2.0  | 2.8            | 1.7  | +0.3                           |          |
| Rock (>15 cm, long axis)                             | 4.7        | 2.6  | 5.8            | 3.1  | –1.1                           |          |
| Slope (%)                                            | 6.3        | 5.1  | 7.4            | 7.5  | –1.1                           | 0.50‡    |
| No. shrubs/saplings intercepted by<br>430-m transect | 39         | 42   | 36             | 35   | +3.2                           | 0.53‡    |
| Canopy closure (%)                                   | 48.3       | 11.0 | 43.1           | 8.4  | +5.3                           | 0.006‡   |
| No. large snags/ha                                   | 4.4        | 4.0  | 3.2            | 2.0  | +1.2                           | 0.17‡    |
| No. small snags/ha                                   | 29.6       | 59.6 | 20.4           | 24.4 | +9.6                           | 0.61‡    |
| No. large logs/ha                                    | 17.6       | 8.4  | 18.8           | 8.8  | –1.2                           | 0.33‡    |
| No. small logs/ha                                    | 30.8       | 16.8 | 26.8           | 12.0 | +4.4                           | 0.27‡    |
| No. trees/ha                                         |            |      |                |      |                                |          |
| Total no. trees (>10 cm dbh)                         | 614        | 270  | 478            | 188  | +136                           | 0.001‡   |
| No. trees 0–20.3 cm dbh                              | 761        | 540  | 658            | 453  | +103                           | 0.12‡    |
| No. trees 20.4–40.6 cm dbh                           | 259        | 82   | 213            | 60   | +46                            | 0.025‡   |
| No. trees >40.6 cm dbh                               | 52         | 26   | 30             | 17   | +21                            | <0.0005‡ |

† Compositional analysis using MANOVA of log ratio-transformed percentages ( $df = 4, 12$  for aspect and ground cover;  $df = 3, 13$  for topographic position).

‡ Two-tailed, paired-sample *t* test ( $df = 15$ ) of the null hypothesis that the mean difference is zero.

cover at ground level, and only 5% of all plots had >36% grass–forb cover.

As suggested by the scatterplots (Figs. 1 and 2), goshawks showed no sex differences in habitat selection. In addition, two-tailed *t* tests indicated that the mean difference for males equaled the mean difference for females ( $df = 14$ , all  $P > 0.05$ ), except for shrub density ( $P = 0.02$ , with females using plots that had 12 more shrubs per 430-m transect than did contrast plots, and males using plots with 11 fewer shrubs per transect than on contrast plots).

Despite selection for dense vegetation structure and large trees, not all used plots were dense stands of large, mature timber (Fig. 3). All used plots had >90 small (<20.3 cm dbh) stems/ha, and two used plots were “doghair” thickets, i.e., stands with >900 stems/ha, all <20.3 cm dbh. Nearly 16% of used plots had <250 trees/ha, 30% had canopy closures <40%, and a few had <20% canopy closure (Fig. 3). For all parameters sampled, the range of sites used by goshawks was im-

pressively broad, and comparable to the range found in contrast plots.

## DISCUSSION

Our methods yielded highly accurate locations (average error 22 m, compared to a plot size >1.7 ha) during periods when the focal goshawk was frequently changing location and alternating between  $\approx 30$  s in a horizontal position and about 5 min in a vertical position. Therefore, we believe that our data accurately reflect the habitats in which goshawks foraged. However, we acknowledge that activities other than foraging may have produced this signal pattern in some cases. Nonetheless, this is one of only three studies in North America to examine how goshawks select habitat for any activity other than nesting, and the only study to include prey density as a habitat element.

Within their home ranges, differences in prey abundance among sites did not appear to influence goshawks in their selection of foraging sites. Although there were

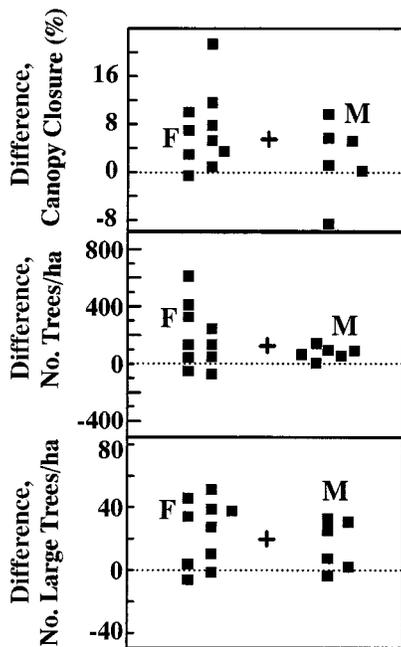


FIG. 2. Differences in canopy closure, total number of trees, and number of large (>40.6 cm dbh) trees/ha between plots used by adult goshawks in northern Arizona during May–September 1993–1994 and paired contrast plots. Each square indicates the mean difference (used – contrast) for one adult female (left,  $n = 10$ ) or one adult male (right,  $n = 6$ ), each with at least two pairs of plots per goshawk; “+” represents the grand mean across 16 goshawks.

fewer medium-sized birds on used plots than on contrast plots, this observation may have little ecological significance, because smaller birds may not be important goshawk prey (Reynolds and Meslow 1984, Boal and Mannan 1994). Mantled ground squirrels, however, are important prey for goshawks, and were clearly not more abundant on used plots than on contrast plots. Similarly, Fischer (1986) found that another North American accipiter, the Cooper’s Hawk (*Accipiter cooperi*), spent more time than expected in oak scrubland, which had the lowest abundance of avian prey of six vegetation types studied, and less time than expected in aspen–maple woodlands, which had the highest abundance of avian prey. Fischer, however, measured prey abundance in vegetation types, not at actual raptor locations.

Our 2.25-ha plot size probably had low power to detect differences in abundance of mammalian prey that occur at low densities, i.e., Abert’s squirrels (which usually occur at densities of <1 squirrel/ha; Patton 1984) and rock squirrels (with low density expected, due to large body size). Although a larger grid may have yielded fewer zero counts and, thus, greater statistical power, prey abundance on a larger plot may be unrelated to the abundance perceived by a goshawk foraging at a particular location within that plot. Indeed, we speculate that goshawks (like researchers)

have difficulty assessing the abundance of low-density prey species on a fine spatial scale.

Our finding that goshawks did not select foraging sites based on prey abundance is limited to third-order habitat selection (Johnson 1980), i.e., selection within the home range. Prey abundance may be an important factor when goshawks locate their home ranges within the larger landscape (second-order habitat selection). This is suggested by the fact that breeding densities of many bird species, including several raptors, increase with food abundance (Newton 1991, 1994).

Goshawks selected foraging sites that had higher canopy closure, greater tree density, and greater density of trees >40.6 cm dbh than on contrast plots. Although the difference between used and contrast plots in canopy closure seems to have little biological significance when mean values are considered (48% vs. 43% closure), this mean difference reflects strong selection for the densest stands (>80% closure) that were least available in the home ranges (Fig. 3). These findings are consistent with the hypothesis that goshawk morphology and behavior are adapted for hunting in moderately dense, mature forests (Mavrogordato 1973:160, Snyder and Snyder 1991).

Previous studies of raptors that forage in open habitats have reported that the availability of perches (Janes 1985, Preston 1990, Widén 1994) and the presence of relatively sparse vegetation at ground level (Wakeley 1978, Baker and Brooks 1981, Bechard 1982, Preston 1990) were more critical than prey abundance

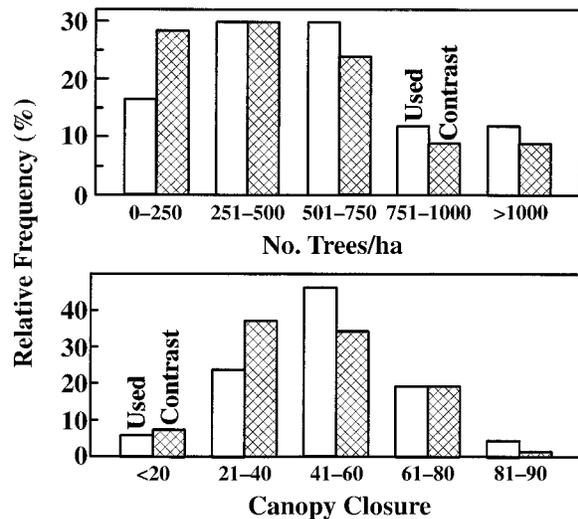


FIG. 3. Relative frequency distribution (%) of tree densities and canopy closures on 67 plots used (open bars) by 20 adult goshawks (including four goshawks for which we sampled one pair of plots per goshawk) in northern Arizona during May–September 1993–1994, and on 67 paired contrast plots (cross-hatched bars). Compositional analyses (using MANOVA of log ratio-transformed percentages;  $df = 4, 12$ ) indicate that the distributions of tree densities do not differ ( $P = 0.15$ ) and the distributions of canopy closures differ ( $P = 0.05$ ) between used and contrast plots.

alone. We suggest that prey *availability* is more important than prey *abundance* in habitat selection by a forest raptor, the goshawk. Obviously, prey numbers are a component of prey availability: if prey are absent, availability must be zero. However, we believe that as long as prey numbers are above a rather low threshold, goshawks select foraging sites where structural characteristics favor their foraging strategies.

Because understory vegetation in ponderosa pine forests is inversely related to tree density (Ffolliott and Clary 1975, and this study) and canopy closure (this study), it is tempting to suggest that goshawks prefer high densities of large trees and highly closed canopies because such stands have more open understories. Although this may be true in forests where the densest understories limit visibility of prey and interfere with goshawk flights, goshawks in the forest we studied selected dense stands of large trees despite a relatively open understory throughout their home ranges. On our study area, it seems more likely that goshawks prefer vegetation that permits them to approach prey unseen and to use their flight maneuverability to advantage, as hypothesized by Widén (1989).

Despite these preferences, the range of stem densities, stem sizes, and canopy closures at sites used by goshawks was strikingly broad. Kenward (1982), Widén (1989), Austin (1993), Bright-Smith and Mannan (1994), and Hargis et al. (1994), also reported similar preferences for large trees or dense forest conditions, and similar tolerance for a broad range of forest structures. We suspect that goshawks used all types of forest stands, in part because of the limited availability of denser stands of large trees in our study area. This is supported by the fact that 55% of the ponderosa pine and mixed-conifer stands in the national forests of Arizona and New Mexico are dominated by trees 12.7–30.5 cm dbh (USDA Forest Service Region 3, Albuquerque, New Mexico, *unpublished data*), making it difficult for a goshawk to maintain a 2400-ha home range (Reynolds et al. 1992) solely in large, dense timber. Furthermore, the only radio-tagged goshawk in our study whose home range was dominated by larger trees had the smallest home range (during the breeding season) of all our radio-tagged goshawks (P. Beier, *unpublished data*). Nonetheless, goshawks exhibit flexible hunting strategies (Kenward and Widén 1989) and probably would use a variety of microsites even if dense stands of large trees were more widely available.

#### *Management implications*

U.S. Forest Service prescriptions for goshawk habitat were designed to support abundant populations of 14 primary prey species (Reynolds et al. 1992). Although our findings suggest that forest structure is more important than prey abundance, Forest Service recommendations should improve conditions for goshawk foraging because they prescribe that 40% of the landscape should be in stands dominated by trees >45.7

cm dbh, and 60% in stands dominated by trees >30.5 cm dbh (Reynolds et al. 1992). Because trees <30.5 cm dbh dominate most ponderosa pine forests in the southwest, the recommendations of Reynolds et al. (1992) should simultaneously improve prey abundance and foraging conditions.

Forest Service recommendations also prescribe a minimum 40% canopy closure in most ponderosa pine areas managed for goshawks (Reynolds et al. 1992). Managing for canopy closures of 40–100% is consistent with our findings of a mean canopy closure of 48% on used plots, aversion to canopy closures <40%, and preference for sites with canopy closure >80%. In some cases, however, these recommendations have been implemented as if 40% were the target instead of a minimum (Arizona Game and Fish 1993). We suggest that goshawk foraging will best be enhanced if managers implement the 40% canopy closure as a true minimum and create a diversity of canopy closures above this minimum, including >60% canopy closures in at least 20% of the area.

In northern Arizona's ponderosa pine forests, most goshawks are year-round residents (P. Beier, *unpublished data*). During winter, goshawks are under greater thermal stress, most avian prey have migrated, and most mammalian prey are hibernating. Under these very different conditions, goshawks may select foraging habitats that differ markedly from those we described for the breeding season. We recommend that winter habitat selection receive top priority for future research on goshawks.

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