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EFFECTS OF PREY ABUNDANCE ON BREEDING SEASON DIET OF NORTHERN GOSHAWKS (*ACCIPITER GENTILIS*) WITHIN AN UNUSUAL PREY LANDSCAPE

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ABSTRACT.—A critical element of diet analysis is species adaptability to alternative prey sources. The breeding-season diet of Northern Goshawks (*Accipiter gentilis*) includes both mammalian and avian species, varies geographically, and is often dependent upon tree squirrels of the genera *Sciurus* and *Tamiasciurus*. We studied alternative prey sources of Northern Goshawks in the South Hills of south-central Idaho, an area where tree squirrels are naturally absent and other prey frequently important in the diet of goshawks, such as smaller corvids, are uncommon. We quantified the diet of goshawks using nest cameras and surveyed abundance of prey using line transects. We found that goshawks consumed roughly 18.5% birds and 78.7% mammals by biomass, with diet dominated by the Belding's ground squirrel (*Urocitellus beldingi*, also known as *Spermophilus beldingi*; 74.8% of total biomass consumed); however, the percentages of mammals and birds in the diet varied between years. The diet was low in diversity, with high overlap among nests, indicating a strong local dependence on the dominant food item. Lastly, the proportion of mammalian prey in the diet was greater in larger broods than in smaller broods. This study provides new insight into the adaptability of the goshawk, particularly in areas with unique prey assemblages.

KEY WORDS: Northern Goshawk; Accipiter gentilis; alternative prey; breeding ecology; diet; Idaho.

EFECTOS DE LA ABUNDANCIA DE PRESAS EN LA DIETA DURANTE LA ÉPOCA REPRODUCTIVA DE ACCIPITER GENTILIS DENTRO DE UN PAISAJE INUSUAL DE PRESAS

RESUMEN.—Un elemento crítico del análisis de la dieta es la adaptabilidad de las especies a fuentes de presa alternativas. La dieta de la estación reproductiva de *Accipiter gentilis* varía geográficamente e incluye especies de mamíferos y aves, y depende a menudo de ardillas arborícolas de los géneros *Sciurus y Tamiasciurus*. Estudiamos fuentes de presa alternativas de *A. gentilis* en las South Hills del centro sur de Idaho, un área donde las ardillas arborícolas están naturalmente ausentes y donde son poco comunes otras presas frecuentemente importantes en la dieta de *A. gentilis*, como córvidos más pequeños. Cuantificamos la dieta de *A. gentilis* colocando cámaras en los nidos y medimos la abundancia de presas usando transectas lineales. Encontramos que los individuos de *A. gentilis* consumieron aproximadamente 18.5% de aves y 78.7% de

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mamíferos en términos de biomasa, con una dieta dominada por la ardilla *Urocitellus beldingi*, también conocida como *Spermophilus beldingi* (74.8% de la biomasa total consumida). Sin embargo, los porcentajes de mamíferos y aves en la dieta variaron entre años. La dieta fue poco diversa, con un elevado solapamiento entre nidos, indicando una fuerte dependencia local en la presa dominante. Por último, la proporción de presas de mamíferos en la dieta fue mayor en las nidadas más grandes que en las pequeñas. Este estudio brinda una nueva perspectiva sobre la adaptabilidad de *A. gentilis*, particularmente en áreas con un ensamble de presa único.

[Traducción del equipo editorial]

A species both defines and is defined by the niche it occupies (Colwell and Rangel 2009) and the specific food habits of a species are an important defining quality of its niche. Diet can affect growth and survival at an individual level (Şekercioğlu et al. 2004) and carrying capacity at a population level (Goss-Custard et al. 2002), is an important factor in breeding success (Graham et al. 1995) and nutritional balance (Dierenfeld et al. 1989, Carnarius et al. 2008), and can even influence pigmentation and the immune system (Sternalski et al. 2012). At a community level, predators can affect both abundance and diversity of other species in the ecosystem (Fryxell and Lundberg 1994, Sergio et al. 2006).

Species conservation plans require a comprehensive understanding of the role each species plays in an ecosystem. This includes understanding the diet of each species and how fluctuations in food availability affect survival and reproduction. Furthermore, it is important to understand the flexibility a consumer may express relative to alternative prey sources. As a result, conservation and management plans for raptors have increasingly focused on prey availability in addition to habitat structure (Reynolds et al. 1992, Driscoll and Lindenmayer 2011).

Conservation plans often focus on a few charismatic species to measure the health of an entire ecosystem (Seddon and Leech 2008, Caro and Girling 2010). Top predators, specifically raptors, can be valuable for predicting species abundance and diversity (Sergio et al. 2006); however, the use of a single species as an umbrella management species requires a thorough analysis of the ecology of that species and its interaction with co-occurring species (Seddon and Leech 2008, Caro and Girling 2010).

The Northern Goshawk (*Accipiter gentilis*; hereafter "goshawk") is a generalist predator occupying boreal and temperate forests of the Holarctic (Squires and Reynolds 1997). The diet of the goshawk has been studied in many areas and has shown to be variable, but with a number of avian and mammalian genera consistently represented. The diet of

goshawks during the breeding season usually includes items from the mammalian genera Lepus, Sylvilagus, Sciurus, Tamiasciurus, and Spermophilus, and avian genera Turdus, Colaptes, and Cyanocitta (Boal and Mannan 1994, Bull and Hohmann 1994, Doyle and Smith 1994, Reynolds et al. 1994, Younk and Bechard 1994, Smithers et al. 2005, Lewis et al. 2006, Salafsky et al. 2007). Goshawk breeding season diet is usually dominated by mammalian prey (Bull and Hohmann 1994, Boal and Mannan 1994, Doyle and Smith 1994, Reynolds et al. 1994, Younk and Bechard 1994, Rogers et al. 2005, Smithers et al. 2005), although in southeast Alaska, avian prey made up the majority of the prey (Lewis et al. 2006). With this regional variability in goshawk diet, it is important that local and regional variation be explored.

Goshawk diet has been studied in a number of ways, including pellet analysis (Bull and Hohmann 1994, Younk and Bechard 1994), prey remains analysis (Bull and Hohmann 1994), direct observation (Boal and Mannan 1994), and video surveillance (Rogers et al. 2005, Smithers et al. 2005, Lewis et al. 2006). In a comparison of methods, Lewis et al. (2004) found that video surveillance provided a more complete understanding of diet than the analysis of prey remains or pellets.

The Sawtooth National Forest in south-central Idaho is evaluating the applicability of the Northern Goshawk as a local management indicator species within the forest to help gauge the effects of forest management practices (D. Santini pers. comm., Owen 2010). The objective of this study was to determine the food habits of goshawks for inclusion into the wildlife conservation planning process within the Sawtooth National Forest. We quantified the diet of goshawks during the breeding season in a unique prey landscape to better understand the interrelationships between predator and prey and to identify any potential conservation issues for this sensitive species (Kennedy 2003).

The Cassia section of the Sawtooth National Forest is unique in its natural absence of tree squirrels

of the genera Sciurus and Tamiasciurus (Benkman et al. 2001). The absence of tree squirrels in the area is attributable to the local geology, which has formed small isolated mountain ranges with isolated forests (Benkman et al. 2001). The separation from more contiguous forests limits recolonization after local extinction events (MacArthur and Wilson 1967). Furthermore, smaller members of the family Corvidae such as the Steller's Jay (Cyanocitta stelleri) and the Black-billed Magpie (Pica hudsonia) are uncommon in the area (R. Miller unpubl. data). Prev availability for goshawks in this region is therefore distinct from other areas where breeding season diet has been studied, with the possible exception of northern Nevada (Younk and Bechard 1994), where tree squirrels were also absent. We hypothesized that mammalian prey would be the dominant prey source, as in most other studies, and the lack of tree squirrels would be compensated for by an increase in consumption of black-tailed jackrabbit (Lepus californicus), mountain cottontail (Sylvilagus nuttallii), pygmy rabbit (Brachylagus idahoensis), Belding's ground squirrels, and golden-mantled ground squirrels (Spermophilus lateralis). Furthermore, we hypothesized that an increase in consumption of American Robin (Turdus migratorius), woodpeckers (Sphyrapicus spp., Picoides spp., Colaptes spp.), and grouse (Bonasa spp., Centrocercus spp., Dendragapus spp., Tympanuchus spp.) would compensate for the lack of smaller corvids. Lastly, we hypothesized that differences in prey abundance among individual goshawk territories would translate into different dietary composition among nests.

METHODS

Study Site. The study site encompassed the Cassia section of the Minidoka Ranger District of the Sawtooth National Forest in south-central Idaho $(41^{\circ}58.8'-42^{\circ}19.8'N, 113^{\circ}58.8'-114^{\circ}28.8'W; Eleva$ tion: 1468-2456 m). The section occupies portions of Twin Falls and Cassia counties. The Cassia section contains approximately 125 000 ha and is bordered primarily by Bureau of Land Management lands (U.S. Forest Service 2003). The naturally fragmented forest is dominated by grasslands and mountain big sagebrush (Artemisia tridentata vaseyana; approximately 80%; U.S. Forest Service 1980). The remaining forested landscape consists predominantly of aspen (Populus tremuloides), lodgepole pine (Pinus contorta), and subalpine fir (Abies lasiocarpa; U.S. Forest Service 1980). Most habitat components within the study area are functioning "at risk" or "not functioning properly" bringing the long-term viability of the ecological functions that they provide into question (U.S. Forest Service 2003). These "at risk" components include sagebrush (threatened by invasive weeds and grasses and altered fire regime), aspen (die-off without regeneration, replacement by other species), lodgepole pine (fire suppression, insects, and disease), and riparian (grazing and dispersed recreation; U.S. Forest Service 2003). Limited timber harvesting occurs in the area (U.S. Forest Service 2003).

Reproductive Terminology. We considered a nest occupied if we observed an adult or subadult goshawk on a nest in brooding posture on at least two separate visits to the area (Woodbridge and Hargis 2006). We aged nestlings visually with the help of a photographic key (Boal 1994). We considered a nest successful if at least one nestling reached an age of 35 d (Woodbridge and Hargis 2006). We defined productivity as the number of young per successful nest that reached an age of at least 35 d.

Goshawk Nests. We discovered goshawk nests by searching historical nesting territories and additional areas prioritized using geographic information system analysis (Reich et al. 2004, Miller et al. 2013). We searched by first checking historical nest structures to see if they were occupied, and if not, then searching on foot within 300 m of historical nesting structures for new nests. If we still failed to locate an occupied nest in the area, we then broadcast alarm calls to solicit a response every 300 m out to the 1370 m (588 ha area) approximated male home range from historical nest structures (Woodbridge and Hargis 2006). We used an average male home range of 588 ha, based on prior radiotelemetry in the same study area (Hasselblad et al. 2007). Only a single set of broadcast surveys were performed, which has been shown to be 70% effective in detecting occupied goshawk nests (Woodbridge and Hargis 2006); however, repeat visits and detections were recorded when we were in the area for other purposes such as prey survey transects.

Nest Cameras. We quantified the diet of goshawks using nest cameras. We installed three cameras each year, including one analog and two digital cameras in 2011 and three digital cameras in 2012 (Table 1). We selected nests for cameras based on timing, location, and access. We stratified the study area into four regions, each with unique characteristics (west, central, east, south), primarily to prevent spatial autocorrelation and to control for experimental error. The west stratum consisted of sagebrush/

Table 1. Summary of footage acquired from cameras placed at six nestling-phase nests of Northern Goshawks within the Sawtooth National Forest in south-central Idaho in 2011 and 2012. Hours of footage recorded from nestlings that had reached approximately 10 d old until they fledged (percent of day-light time successfully recorded between nestlings age 10 d and fledging in parentheses).

NEST ID/ YEAR	STRATUM	NESTLINGS	DIGITAL/ ANALOG	DATE Installed	AGE AT Install	DATE OF LAST FOOTAGE	Hours of Footage
DFJ-2011	Central	2	A	June 14	10 d	July 9	240 (50%)
PC-2011	South	2	D	June 18	17 d	July 10	346 (72%)
TS-2011	West	1	D	June 8	14 d	July 4	281 (59%)
BPS-2012	East	3	D	June 13	14 d	July 14	428 (79%)
CS-2012	West	4	D	June 12	12 d	July 13	235 (43%)
ECS-2012	Central	3	D	June 12	9 d	July 17	456 (95%)

grass communities with isolated islands of aspen and lodgepole pine. The central stratum consisted of fragmented lodgepole pine, subalpine fir and aspen stands separated by sagebrush grass communities. The east stratum was dominated by rock, grass, and sagebrush with isolated pockets of mostly lodgepole pine. The south stratum was also dominated by sagebrush/grass communities with isolated patches of lodgepole pine, aspen, subalpine fir, and pinyonjuniper (U.S. Forest Service 2003). We randomly selected candidate nests in each region from a pool of occupied nests that did not pose logistical constraints for installation of cameras. We omitted nests from the study if the tree could not be climbed safely, if the territory had hosted a camera the previous year, or if the nest was discovered after a camera had already been placed in that stratum for that year.

Cameras were either analog or digital and had at least a 60-m cable allowing remote battery and tape/memory exchange to minimize disturbance to nesting goshawks (Rogers et al. 2005). All recording occurred during daylight hours (0545 H and 2145 H local time), at a rate of at least two frames per second. We made best efforts to maintain daily recording from a nestling age of 10 d through fledging. Complete recording coverage was limited by battery recharge/replacement logistics, livestock chewing through video cables, and human sabotage.

We climbed nest trees using climbing spurs or climbing a rope shot over a branch near the nest. We positioned cameras as close as possible to the nest bowl to view the entire nest from a 45° or higher angle (Rogers et al. 2005). We had a minimum of three crew members for each camera installation, which allowed us to minimize disturbance time to <60 min per nest. We removed cameras after the nestlings had fledged and left the immediate nest area.

Diet Quantification. We reviewed all recorded video to determine the number and biomass of prey deliveries. We logged the nest name and video timestamp and identified the class, species, age, and size of prey delivered based on the relative size compared to the head of the adult. Size categories included small, medium, and large prey each for avian and mammalian prey. Prey deliveries were identified to class and to genus and species when possible using researcher knowledge of species and reference materials (Whitaker et al. 1980, Harrison 1987, Udvardy et al. 1994, Sibley 2003).

We calculated biomass consumed at the nest using species mass information obtained from Sibley (2003) and Whitaker et al. (1980). For mammalian prey species, we classified individuals as juveniles or adults based on size and used one-half the adult mass to represent juvenile mammalian mass (Bielefeldt et al. 1992). For avian prey species, we classified individuals as nestlings, juveniles, or adults (Reynolds and Meslow 1984). We used 100% of adult mass for small birds (e.g., Junco spp.), 65% and 95% for medium-sized birds (e.g., Turdus spp., Pipilo spp.), and 55% and 95% for large birds (e.g., Bonasa spp., Asio spp.) for estimating mass of nestlings and juveniles, respectively. For unidentified prey items, we used the average biomass of the identified prey items based on estimated size and adjusted this value for the amount of time required to consume the prey. For example, a large prey item that required 15 min to consume was assigned a mass of 120 g, and a small prey item that required only 3 min to consume was assigned a mass of 25 g. This approach was qualitatively calibrated by observing consumption times for identified prey

For among-nest comparisons we calculated a prey delivery rate by count and by biomass based on total

deliveries during the season and total amount of video captured for each nest. We used the number of young that successfully reached an age of 35 d as the measure of brood size (Woodbridge and Hargis 2006). There was no in-nest mortality observed after camera installation. We measured the effect of brood size on prey deliveries, biomass delivered, biomass delivered per nestling, proportion of prey deliveries that were mammals, and the portion of biomass delivered that was mammalian with linear models with year always included as a fixed effect. We compared models with brood size and year as predictors against the model with only year as a predictor ("null" model) using an analysis of deviance test (Zuur et al. 2009). We evaluated the appropriateness of the chosen models by inspecting the distribution of model residuals when plotted against the fitted values (Zuur et al. 2009). We calculated the change in proportion of mammals consumed through the seasons by only including days where complete video coverage was acquired for a given nest. We evaluated the change in brood size between years with generalized linear models assuming a Poisson distribution.

We calculated prey diversity using prey items identified to genus or species level with an inverse form of the Simpson Diversity Index (1/D; Simpson 1949, Smithers et al. 2005). As not all prey items were identified to genus or species, the diversity indices are biased lower. We measured prey diversity on a study-wide scale and also on a nest scale. We compared year-to-year variation in prey diversity using a two-sample Student's t-test (Zar 2010). We calculated diet overlap among nests using a Simplified Morisita's Index of Overlap (Krebs 1999, Smithers et al. 2005). The overlap index scales between zero and one, with one indicating complete overlap. Both prey indices are more heavily influenced by dominant species within the diet than items only occurring on a few occasions. We compared productivity between years using generalized linear models with a Poisson distribution (Zar 2010).

Prey Abundance. We estimated prey abundance in each territory using distance sampling along line transects (Buckland et al. 2001). We overlaid four random transects, each 750 m in length, within the 588-ha assumed male home range of each nest. We chose four separate surveys per territory instead of repeated surveys to increase the coverage area of the territory at the expense of enabling separate analysis of abundance and availability (Buckland et al. 2004, Salafsky et al. 2007).

Each transect was surveyed between 0730 H and 1130 H local time during the nesting season. We used best efforts to distribute the surveys during the entire nesting season, among different surveyors, and at different times of day. We walked each transect noting all potential prey items large enough to have an important influence on diet. We recorded all mammals ranging from chipmunk-size to jackrabbit-size and all birds from towhee-size (i.e., 30 g) to grouse-size. We detected prey by sight or sound. We used a laser rangefinder to measure the perpendicular distance from the line to the location where the prey item was first observed, or if heard only, the estimated location (Buckland et al. 2001).

We analyzed prey abundance separately by class Aves and class Mammalia. Observation distances were grouped into bins of 10 m and truncated to 80 m for avian detections and 60 m for mammalian detections to smooth the detection curves and decrease the influence of outliers (Buckland et al. 2001). We fitted separate detection curves by year and by class using half-normal and hazard-rate curve shapes, all survey results from the entire study area, and detection covariates including surveyor, day-ofyear, time-of-day, and the percent of the transect that was in open-canopied habitat versus closedcanopied habitat (Buckland et al. 2004). We performed separate analysis by year to better detect year to year changes in prey abundance. We chose the top model by using various combinations of the two model shapes and the four covariates as predictor variables against the survey results using AIC (Burnham and Anderson 2002, Buckland et al. 2004). We applied this top model to the individual survey results for each territory with a nest camera to produce an estimated abundance of avian prey and a separate estimate of abundance of mammalian prey for each territory. These estimates are indices and not true estimates of abundance as we did not compensate for availability via repeat surveys or adjustments for species or sex differences in detectability (i.e., only detecting males singing or only detecting ground squirrels above ground). Lastly, we compared the proportion of the prey deliveries that were mammalian with the mammalian and avian abundance indices for each territory using linear models. We compared models with abundance and year as predictors against the model only including year ("null" model) using an analysis of deviance test (Zuur et al. 2009). We evaluated the appropriateness of the chosen models by inspecting the distribution of model residuals when plotted against the fitted values (Zuur et al. 2009).

We used an alpha value of 0.05 to measure significance in all frequentist statistical tests (t-test and generalized mixed models). We reported all means with \pm SE. We conducted all statistical analyses in R (R Development Core Team 2011). We calculated the Simpson Diversity Index and the Simplified Morisita Index of Overlap with the R library "vegan" (Oksanen et al. 2012). We calculated prey abundance via distance sampling using the R library "unmarked" (Fiske and Chandler 2011).

RESULTS

We successfully used six nest cameras to quantify the diet of breeding season goshawks, three cameras each year. Total disturbance time associated with nest camera installation averaged 47 ± 4.0 min per nest (range 33 to 58 min). We recorded 1995 hr of usable footage on 141 "nest-days," representing 66% of daylight coverage of nestlings aged 10 d to fledging (Table 1). We recorded 657 prey deliveries: 260 items in 2011 and 397 items in 2012 (Tables 2, 3). We identified 96% of prey items to class and 74% to genus or species (Tables 2, 3). In 2011, we classified 46.2% of prey deliveries as mammals, 50.8% as birds, and 3% remained unclassified. In 2012, we classified 75.8% as mammals, 19.6% as birds, and 4.6% remained unclassified. The items unidentifiable to species were disproportionately birds as they were often plucked or decapitated before delivery, were often nestlings, and because they were consumed much more quickly. Based on estimations of prey biomass, we calculated that mammalian and avian prey made up 67.4% and 29.9%, respectively, in 2011, and 85.2% and 11.9%, respectively, in 2012 of the diet of goshawks (Tables 2, 3).

Prey deliveries averaged 0.33 ± 0.02 items per daylight hour overall, 0.30 ± 0.01 in 2011 and 0.35 ± 0.02 in 2012. Prey biomass deliveries averaged 40.2 ± 3.4 grams per daylight hour overall, 34.0 ± 1.2 in 2011 and 46.4 ± 4.2 in 2012. The average biomass per prey delivery was 122.9 ± 2.3 g. Prey delivery rates did not vary with the size of the brood ($F_1 = 2.27$, P = 0.23); nor did biomass delivery rates ($F_1 = 1.11$, P = 0.37). The one singlenestling brood averaged 18.1 g per daylight hour, two-nestling broods averaged 17.5 ± 0.6 g per nestling per daylight hour, three-nestling broods averaged 14.7 ± 2.0 g per nestling per daylight hour, and the four-nestling brood averaged 12.7 g per nestling per daylight hour; biomass delivered per nestling did not vary with brood size $(F_1 = 4.46, P$ = 0.13). These results are biased as adults often consumed prey while feeding nestlings and this behavior was observed more often in the smaller brood nests.

The proportion of prey deliveries that were mammals for the single-nestling brood was 0.49, two-nestling broods averaged 0.45 \pm 0.01, three-nestling broods averaged 0.80 \pm 0.00, and the four-nestling brood was 0.77. The proportion of prey deliveries that were mammalian varied by brood size (F_1 = 15.61, P = 0.03) as did the proportion of biomass that was mammalian (F_1 = 59.19, P = 0.005). Mammalian prey biomass delivered to nests peaked during the third week of the season, then slowly trended lower, but this decrease was only evident in 2012 (Fig. 1).

Based upon identified prey deliveries, the measure of prey diversity for all six nests was 1.52. Values among nests ranged from 1.27 to 2.02 with a mean value of 1.67 \pm 0.13. Prey diversity varied between years with a mean of 1.94 \pm 0.05 in 2011 (range 1.86 to 2.02) and a mean of 1.40 \pm 0.11 in 2012 (range 1.27 to 1.61; \pm test_{2.75} = 4.68, P = 0.02). Dietary overlap among nests averaged 0.974 \pm 0.00 (range 0.947 to 0.996; Table 4). Dietary overlap among nests in 2011 averaged 0.977 \pm 0.01, whereas in 2012 it averaged 0.991 \pm 0.00.

Across the study area, we found a numerically higher number of occupied nests (19 nests in 27 territories vs. 10 nests in 24 territories) and generally larger average number of fledglings per successful nest (productivity; 2.42 ± 0.25 vs. 2.12 ± 0.3) in 2012 than in 2011, although the difference is not significant (Z=0.46, P=0.65). Two of the ten nests in 2011 failed for unknown reasons, while all 19 nests in 2012 were successful. There were no failures or in-nest mortality within nests hosting cameras after the cameras were installed.

To analyze prey abundance across the study area, we completed 96 surveys in 24 territories in 2011 with two surveyors and 108 surveys in 27 territories in 2012 with three surveyors, for 204 total prey surveys encompassing 149 851 m of survey. Prey surveys were conducted between 3 June and 13 July in 2011, and 29 May and 12 July in 2012. We observed 1485 potential prey items that met our size criteria for inclusion in analyses. We fit a half-normal detection curve for both avian and mammalian prey using distance sampling techniques. The top model for avian detection in both years was based only on the covariate for surveyor. The top model for mammalian detection in both years was based on the

Table 2. Prey items delivered to three nestling-phase nests of Northern Goshawks within the Sawtooth National Forest in south-central Idaho in 2011. Footage recorded using nest cameras within nests where nestlings had reached approximately 10 d old until they fledged. Count represents the number of unique prey deliveries represented by each species or category. % Items represent the percentage of total prey deliveries represented by the count. % Biomass represents the percent of total estimated biomass by each species or category.

CLASS	SPECIES	COUNT	% ITEMS	% BIOMASS
Mammalia	Belding's ground squirrel (<i>Urocitellus beldingi</i>)	97	37.3%	58.3%
Mammalia	Golden-mantled ground squirrel			
	(Callospermophilus lateralis)	1	0.4%	0.8%
Mammalia	Chipmunks (<i>Tamias</i> spp.)	2	0.8%	0.3%
Mammalia	Ord's kangaroo rat (Dipodomys ordii)	1	0.4%	0.2%
Mammalia	North American deermouse (Peromyscus			
	maniculatus)	1	0.4%	0.1%
Mammalia	Unknown	18	6.9%	7.6%
	Total Mammalia	120	46.2%	$\boldsymbol{67.4\%}$
Aves	Northern Flicker (Colaptes auratus)	12	4.6%	5.2%
Aves	American Robin (Turdus migratorius)	14	5.4%	3.3%
Aves	Common Raven (Corvus corax)	1	0.4%	2.2%
Aves	Long-eared Owl (Asio otus)	2	0.8%	1.0%
Aves	Hairy Woodpecker (Picoides villosus)	2	0.8%	0.4%
Aves	Spotted Towhee (Pipilo maculatus)	3	1.2%	0.4%
Aves	Western Meadowlark (Sturnella neglecta)	1	0.4%	0.3%
Aves	Dark-eyed Junco (Junco hyemalis)	2	0.8%	0.1%
Aves	Unknown	95	36.5%	16.9%
	Total Aves	132	50.8%	29.9%
Unknown	Unknown	8	3.0%	2.7%

covariates for surveyor and the percent of the transect in open habitat. Of all completed surveys, 58.4 \pm 2.13% of the survey distance fell within open-canopied habitat.

Prey abundance varied numerically between years and among territories. Across the study area, mammalian abundance was estimated at 0.79 ± 0.08 individuals per ha in 2011 and 0.85 ± 0.06 individuals per ha in 2012. Study-wide avian abundance was estimated at 0.57 ± 0.04 individuals per ha in 2011 and 1.22 ± 0.06 individuals per ha in 2012. Mammalian abundance estimates within the territories having nest cameras ranged from 0.24 ± 0.17 individuals per ha to 1.54 ± 0.39 individuals per ha, with a mean of 0.64. Mammalian abundance was not correlated with the proportion of mammalian prey deliveries (F_1 = 5.26, P = 0.11). Avian abundance estimates within territories hosting nest cameras ranged from 0.57 ± 0.16 individuals per ha to 1.50 ± 0.30 individuals per ha, with a mean of 1.02. Avian abundance was not correlated with the proportion of mammalian prey deliveries, as the model with only year as a predictor outperformed the model with avian abundance and year as a predictor.

DISCUSSION

Mammals dominated the breeding season diet for goshawks in our study area (78.7% of total biomass delivered), which was consistent with most other goshawk studies. However, in 2011 the total number of avian prey items delivered, but not biomass delivered, did exceed the number of mammals delivered (Table 2). Consistent with our first hypothesis, in the absence of tree squirrels, the dominant prey delivered to nests was the Belding's ground squirrel (Urocitellus beldingi, also known as Spermophilus beldingi; 59.7% of items, 74.8% of biomass; Tables 2, 3). Our results are consistent with those of Younk and Bechard (1994) in northern Nevada, an area with similar habitat and forest structure (high-elevation shrubsteppe with highly fragmented forest stands) that also lacks tree squirrels. Consistent with our second hypothesis, the goshawks appeared to compensate for the lack of smaller corvids by eating woodpeckers, robins, and to a lesser degree, grouse (Tables 2, 3).

The number of prey deliveries and biomass delivered per day did not vary with brood size; however, the proportion of mammals in the diet did increase

Table 3. Prey items delivered to three nestling-phase nests of Northern Goshawks within the Sawtooth National Forest in south-central Idaho in 2012. Footage recorded using nest cameras within nests where nestlings had reached approximately 10 d old until they fledged. Count represents the number of unique prey deliveries represented by each species or category. % Items represent the percentage of total prey deliveries represented by the count. % Biomass represents the percent of total estimated biomass by each species or category.

CLASS	Species		% ITEMS	% BIOMASS
Mammalia	Belding's ground squirrel (<i>Urocitellus beldingi</i>)	295	74.3%	84.2%
Mammalia	Golden-mantled ground squirrel			
	(Callospermophilus lateralis)	2	0.5%	0.4%
Mammalia	Chipmunk (Tamias spp.)	1	0.3%	0.1%
Mammalia	North American deermouse (Peromyscus			
	maniculatus)	1	0.3%	0.1%
Mammalia	Short-tailed weasel (Mustela erminea)	1	0.3%	0.2%
Mammalia	unknown	1	0.3%	0.1%
	Total Mammalia	301	75.8%	85.2%
Aves	Northern Flicker (Colaptes auratus)	23	5.8%	5.6%
Aves	American Robin (Turdus migratorius)	9	2.3%	1.3%
Aves	Dark-eyed Junco (Junco hyemalis)	3	0.8%	0.1%
Aves	Ruffed Grouse (Bonasa umbellus)	5	1.3%	1.5%
Aves	Hairy Woodpecker (Picoides villosus)	2	0.5%	0.2%
Aves	Red-breasted Nuthatch (Sitta canadensis)	2	0.5%	0.0%
Aves	White-crowned Sparrow (Zonotrichia leucophrys)	2	0.5%	0.1%
Aves	Western Tanager (Piranga ludoviciana)	1	0.3%	0.1%
Aves	unknown	31	7.8%	3.0%
	Total Aves	78	19.6%	11.9%
Unknown	unknown	18	4.5%	2.9%

with brood size. This higher rate of mammalian consumption may reflect the fact that the higher food demands of larger broods may not be met with relatively smaller avian prey items. However, even large broods continued to receive some deliveries of relatively smaller avian prey. Although we did not test this hypothesis, this may indicate that dietary diversity is important in this species to maintain specific nutritional requirements (Dierenfeld et al. 1989, Carnarius et al. 2008).

The larger broods trended toward higher biomass delivered per nest than smaller broods, but this trend was not significant due to the presence of a strong year effect. This may also reflect the challenge that adult goshawks have in supporting the greater energy demands of larger broods; however, it could also be the result of bias in our measurements occurring when adult females consumed some of the prey within the nest, which was observed more often in nests with fewer nestlings but was not quantified.

The proportion of avian to mammalian biomass shifted away from mammals later in the season, especially in 2012 (Fig. 1). This could be the result of early ground squirrel estivation in 2012 after earlier

ground squirrel emergence (Blake 1972), local depletion of naive juvenile dispersing ground squirrels (Morton and Gallup 1975, Bonal and Aparicio 2008), increased prey consumption by the female outside of the nest versus inside the nest, or a natural decrease of food deliveries as nestlings approach fledging age (Newton 1979).

In evaluating the portion of mammals consumed, we had a large year effect as there was no overlap in brood size in nests hosting cameras between the two years. We therefore included year as a fixed effect in all analyses. With this approach we noted that neither mammalian abundance nor avian abundance within the nesting territory were significant predictors for the delivery rate of mammals, as most of the variance was attributed to the year effect. These results fail to support our third hypothesis that local prey abundance would be a predictor for dietary composition; however, this may be the result of study implementation as we failed to have an overlap in sampled brood size between years.

Dietary diversity within our study was low as measured by the inverse Simpson's Index. Our results are biased by the large number of unidentified avian species which presumably include species not

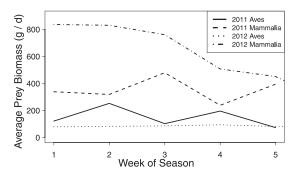


Figure 1. Average prey biomass delivery rates divided by prey class and by year into six nests of Northern Goshawks with nest cameras during the nestling-phase of the breeding season within the Sawtooth National Forest in south-central Idaho for 2011 and 2012. Week of Season indicates weeks since the first day of full video footage captured (i.e., week 1 indicates days 0 thru 6 inclusive since the first day of footage). Averages represent three nests each year and only include days for which a full 16 hr of video coverage were captured.

previously encountered. However, the dominance of ground squirrels in the diet would still constrain this index. Combined with the high degree of dietary overlap between nests, we can conclude that the nest success of the goshawk in this area is strongly dependent upon a single prey species during the nestling phase, the Belding's ground squirrel.

The high dependence of all monitored nests upon the Belding's ground squirrel as a prey source presents some important challenges that likely explain a portion of the year effect we observed in this study. The Belding's ground squirrels only spend about 3–4 mo per year aboveground (Sherman and Morton 1984). They emerge shortly after the snowpack melts and then return underground to estivate starting in July (Morton and Gallup 1975). The timing of emergence may be critically important to goshawk reproductive success in the area. In 2011, the

snow pack within the study area melted nearly 3 wk later than average (7 June), whereas in 2012 it melted 3 wk earlier (26 April) than average (18 May; U.S. Department of Agriculture 2011). Correspondingly, we observed a higher delivery rate of ground squirrels in 2012 than in 2011, which could be the result of late emergence in 2011, although ground squirrels had clearly emerged by the time we installed nest cameras in both years. If annual variation in snowpack melting increases, it's possible that goshawk breeding and prey availability could fail to be fully synchronized, possibly putting this population at risk.

Our study has provided critical information for the evaluation of the goshawk as a management indicator species within the Sawtooth National Forest. Seddon and Leech (2008) reviewed literature and proposed seven criteria for evaluating species as appropriate umbrella management species. The goshawk naturally meets a number of these criteria, such as large home-range size (relative to the forest size), high probability of persistence, co-occurrence with other species of interest, management needs benefit other species, moderate sensitivity to human disturbance, and easily sampled or observed. Additionally, the natural history and ecology of the goshawk is generally well known, but regional variation is common in this species. We have specifically helped fill in the knowledge of the most important criterion—species biology—within this unique prey landscape. This enables a more rigorous assessment of the interwoven food web in which the goshawk participates. The dietary observations highlight the adaptability of the species, but also the critical dependence (ground squirrels) which may be required for their continued success in the area. However, the management actions required to maintain ground squirrel abundance may not be consistent with the needs for overall species diversity.

Table 4. Breeding season dietary overlap comparisons among six nestling-phase nests of Northern Goshawks within the Sawtooth National Forest in south-central Idaho in 2011 and 2012 using Simplified Morisita's Index scaled between zero and one. Zero indicates no diet overlap; one indicates complete overlap.

Nest ID/Year	DFJ-2011	PC-2011	TS-2011	BPS-2012	CS-2012	ECS-2012
DFJ-2011 PC-2011	1	0.961	0.987 0.982	0.963 0.961	0.972 0.981	0.964 0.947
TS-2011 BPS-2012		1	1	0.971	0.982 0.993	0.970 0.996
CS-2012 CS-2012 ECS-2012				1	1	0.985 1

Our study has provided a strong foundation for goshawk conservation within this unique landscape but additional information is required. As Wiens et al. (2006) stated, post-fledging diet and survival are at least equally important as they are during the nestling period. Increased focus on dietary influences earlier in the season before ground squirrels emerge, and later in the season after they estivate, are clearly warranted.

In conclusion, we have confirmed that goshawks in our study area are heavily dependent upon mammalian biomass, primarily in the form of Belding's ground squirrels, and the delivery rate of mammalian prey is higher in larger broods, even when year effects are considered. Our results also showed how adaptive the goshawk can be to alternative prey sources. The low diet diversity and high dietary overlap among nests point to a reliance on a few species, which could make this population of goshawks sensitive to prey population fluctuations.

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