

RED-TAILED HAWK DIETARY OVERLAP WITH NORTHERN GOSHAWKS ON THE KAIBAB PLATEAU, ARIZONA

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ABSTRACT.—We determined food habits of Red-tailed Hawks (*Buteo jamaicensis*) for comparison with published information for Northern Goshawks (*Accipiter gentilis*) to evaluate potential competition on the Kaibab Plateau, Arizona. We collected prey remains and pellets from 42 Red-tailed Hawk nests at the end of the nesting season between August–October 1998–2001, and opportunistically from below nest trees during site visits, May–July 2000–01. We identified 478 prey items, including 17 mammal, 7 bird, and 2 reptile species. Prey species frequency did not vary among years ($P = 0.3$), across habitat types ($P = 0.8$), or by collection technique ($P = 0.4$). Annual food niche breadth for Red-tailed Hawks averaged 0.57. Published mean niche breadth for Northern Goshawks was 0.32, supporting that Red-tailed Hawks were feeding generalists, while Northern Goshawks were more specialized. However, 48% of Red-tailed Hawk diet on the Kaibab Plateau consisted of species comprising a major portion of the documented diet of Northern Goshawks, including Nuttall's cottontail (*Sylvilagus nuttallii*), golden-mantled ground squirrel (*Spermophilus lateralis lateralis*), rock squirrel (*S. variegates grammurus*), and Northern Flicker (*Colaptes auratus*). Because raptor communities with high dietary overlap and lack of prey partitioning show food-limited nesting success, greater agonistic behavior, and territoriality, Red-tailed Hawks could be negatively affecting Northern Goshawks on the Kaibab Plateau.

KEY WORDS: Red-tailed Hawk; *Buteo jamaicensis*; Northern Goshawk; *Accipiter gentilis*; competition; diet; food habits; food niche breadth; foraging.

SOBRELAPAMIENTO DE LA DIETA DE *BUTEO JAMAICENSIS* Y *ACCIPITER GENTILIS* EN LA MESETA DE KAIBAB, ARIZONA

RESUMEN.—Determinamos la dieta de *Buteo jamaicensis* en la planicie de Kaibab, Arizona y la comparamos con información publicada sobre *Accipiter gentilis* con la finalidad de evaluar la posible existencia de competencia entre estas dos especies. Recolectamos restos de presas y egagrópilas de 42 nidos de *B. jamaicensis* al final de la temporada reproductiva entre agosto y octubre de 1998–2001, y de forma oportunista debajo de árboles de anidación durante visitas a la zona de estudio realizadas entre mayo y julio de 2000 y 2001. Identificamos 478 tipos de presas, incluyendo 17 especies de mamíferos, 7 de aves y 2 de reptiles. La frecuencia de las especies de presa no varió entre años ($P = 0.3$), tipos de hábitat ($P = 0.8$) y técnicas de colecta ($P = 0.4$). La amplitud anual del nicho alimentario de *B. jamaicensis* promedió 0.57. Registros publicados indican que la amplitud del nicho alimentario de *A. gentilis* es 0.32, lo cual sugiere que *B. jamaicensis* es una especie generalista, mientras que *A. gentilis* es más especializada. Sin embargo, el 48% de la dieta de *B. jamaicensis* en la planicie de Kaibab consiste de especies que forman la mayor parte de la dieta documentada para *A. gentilis*, entre las que se encuentran *Sylvilagus nuttallii*, *Spermophilus lateralis lateralis*, *S. variegates grammurus* y *Colaptes auratus*. Debido a que las comunidades de rapaces que presentan un alto grado de superposición en su dieta y en las que no hay repartición de presas muestran un bajo éxito de anidación debido a falta de alimento,

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un mayor comportamiento antagónico y mayor territorialidad, *B. jamaicensis* podría estar afectando negativamente a *A. gentilis* en la planicie de Kaibab.

[Traducción del equipo editorial]

Fire suppression, timber harvesting, and livestock grazing over the past 100 yr have caused changes in southwestern forests, including those on the Kaibab Plateau in northwestern Arizona (e.g., Weaver 1951, Cooper 1960, Covington and Moore 1994). Decreasing the quality and quantity of climax forest can favor habitat generalists (Carey 1984) such as Red-tailed Hawks (*Buteo jamaicensis*), which may out compete species dependent on late successional forests, such as Northern Goshawks (*Accipiter gentilis*; Andersen et al. 2003). Creation of 259-ha buffer zones on the plateau by the Kaibab National Forest, although maintaining the quality of old-growth for nesting sites, does not ensure sufficient quantity or quality of old-growth forest beyond these protected areas (Reynolds et al. 1992). Red-tailed Hawks often nest in abandoned Northern Goshawk nests after timber harvesting (Crockner-Bedford 1990). Beyond old-growth-managed buffer zones, open areas may favor the hunting style, and thus, increase foraging habitat of Red-tailed Hawks more than Northern Goshawks. Exploring the potential relationship between these two species facilitates a better understanding of how upper level avian predators have adjusted to human-caused alterations in southwestern forest ecosystems. Further, this understanding could aid resource managers in maintaining a viable Northern Goshawk population on the Kaibab Plateau.

Competition occurs when use or defense of a resource by one individual reduces the availability of that resource to other individuals (Gill 1990). Interspecific competition occurs when individuals of coexisting species require a resource that is in limited supply relative to their needs such that survival or reproduction of at least one species is decreased (Ricklefs and Schluter 1993). On the Kaibab Plateau, Red-tailed Hawks and Northern Goshawks, based on their proximity and similar habitat use, could be competing for nest sites, foraging areas, or prey, despite potential partitioning resulting from morphological and behavioral differences between species (Ballam 1984, Squires and Reynolds 1997). In this study, we focused on determining the diet of Red-tailed Hawks for comparison with published information on Northern Goshawks to evaluate potential overlap. We hypoth-

esized that Red-tailed Hawks and Northern Goshawks, because of their close proximity and use of similar nesting and foraging habitat, could also be using the same prey species, creating the potential for competition.

STUDY AREA

The Kaibab Plateau, on the North Rim of the Grand Canyon, is located in northwestern Arizona within the Kaibab National Forest. The plateau encompasses 2980 km² above 1830 m elevation. Our study area was confined to 1732 km² above the 2075 m contour to be consistent with concurrent long-term Northern Goshawk research on the plateau (Reynolds et al. 1994). Goshawk and Red-tailed Hawk nest sites are interspersed throughout this study area. Vegetation on the plateau consists of ponderosa pine (*Pinus ponderosa*) forest between 2075–2500 m; mixed-conifer forest (ponderosa pine, Douglas-fir [*Pseudotsuga menziesii*], white fir [*Abies concolor*], blue spruce [*Picea pungens*], and quaking aspen [*Populus tremuloides*]) between 2500–2650 m; and Engelmann spruce-subalpine fir (*Picea engelmannii-Abies lasiocarpa*) forest between 2650–2800 m (Rasmussen 1941, White and Vankat 1993).

METHODS

Prey Remains and Pellet Identification. We collected prey remains and regurgitated pellets from all known occupied Red-tailed Hawk nests ($N = 21, 24, 32, 11$ for 1998–2001, respectively), from below and in the nest, at the end of the nesting season, August–October 1998–2001, and opportunistically during the nesting season, May–July 2000–01. Collections from each nest were separated by >3 d, and end-of-season samples were collected >30 d after previous collections. We treated each collection of pellets and prey remains from an occupied nest as one sample for that nest site. We assumed prey species identified in each sample had been consumed since the last sample and represented new prey.

To identify prey, we separated samples into bones/fragments, feathers, and hair. Bones and feathers were identified to the lowest taxon possible, through comparison with S. Bayard's reference prey collection stored at the Rocky Mountain Research Station, Fort Collins, CO. We identified hairs using keys (Williams 1938, Stains 1958, Moore et al. 1974) and by comparing hairs directly with samples from the Northern Arizona University, Department of Biological Sciences' collection and the private collection of H.E. Graham (Flagstaff, AZ U.S.A.). The characteristics we considered included color banding, shape, presence of a hair shield, and configuration of a medulla if present (Moore et al. 1974).

Determining diet via indirect means requires cautious interpretation because of inherent biases associated with each method (Lewis et al. 2004); however, identification of a prey species in pellets and prey remains is an absolute indication of presence. Therefore, we recorded one occurrence whenever a species was found in a sample.

We then pooled samples across years for each nest and summed the number of times a prey species occurred. This provided a conservative estimate of the relative importance of prey species consumed by Red-tailed Hawks at each nest. We also calculated the total number and percent of nests at which each prey species occurred.

Prey Species Dissimilarity. Dyer (1978) developed a linear statistical analysis for comparing species dissimilarity that can be used in conjunction with any species dissimilarity index and is designed for data sets that involve both multiple species and multiple environmental variables. Total species dissimilarity is divided into components with one component being assigned to each environmental variable or interaction of environmental variables:

$$D_{ij} = \beta_0 + \beta_1\delta_{ij}^{(1)} + \beta_2\delta_{ij}^{(2)} + \dots + \beta_m\delta_{ij}^{(m)} + e_{ij},$$

where D_{ij} is the (dis)similarity between observations i and j , $\delta_{ij}^{(1)}$ is a known function of i and j which corresponds to the i^{th} environmental variable or interaction, β_1 is an unknown parameter which represents the contribution of the i^{th} environmental variable or interaction to the total dissimilarity, and e_{ij} is an error term with an expected value of 0.

We used this linear model with the Jaccard dissimilarity index (Krebs 1998) to estimate whether the species identified in prey remains and pellets of Red-tailed Hawks varied among years (1998–2001), vegetation types (ponderosa pine only, mixed conifer with pine dominant, or mixed conifer only), or collection techniques (end of season samples from nest or opportunistic samples collected from below nest trees during nesting season). Jaccard's index is specifically designed for presence-absence data, and because, by definition, rare species are typically absent, rare species have little influence on the value of the index (Krebs 1998). The Jaccard dissimilarity index (D_{ij}) is calculated by:

$$D_{ij} = a/(a + b + c)$$

where a is the number of binary characteristics present in sample i and sample j , b is the number present only in i , and c is the number present only in j . We estimated Dyer's model using the Jaccard index. We used permutation methods (Edington 1995) to estimate a significance level (P -value) for each environmental variable. Statistical tests were significant if $P < 0.05$.

Niche Breadth. Niche breadth and niche overlap are widely applied to analysis of foraging and community ecology to estimate competition (Greene and Jaksic 1983). Niche breadths were calculated according to Levins' (1968) equation:

$$\beta = \frac{1}{\sum p_i^2} \text{ for } i = 1 \text{ to } n$$

where p_i is the proportion of Red-tailed Hawk nests with the i^{th} taxon present. The value of β varies from 1 to n , where n is the number of taxa. If prey taxa occur equally among all nests, then $\beta = n$. Niche-breadth values were standardized and converted to a fraction ranging from 0 to 1 by the equation:

$$\beta_{\text{standard}} = (\beta - 1)/(n - 1).$$

To calculate niche breadth, we created a prey species

list based on pooled prey species present across all occupied Red-tailed Hawk nests by year. This yielded a separate food niche breadth measure for each of the four study years. We also calculated a 95% confidence interval for Red-tailed Hawk niche breadth on the Kaibab Plateau for comparison with calculated niche breadths for Northern Goshawks from other studies.

RESULTS

Pellet and Prey Remain Analysis. Considering each visit's collection of pellets and prey remains as one discreet sample, we obtained 140 prey samples ($N = 80$ end of nesting season, 1998–2001; $N = 60$ opportunistic during nesting season, 2000–01), consisting of 1–10 collections from 42 nests ($\bar{x} = 3.3$). We identified 478 prey items, including at least 17 mammal, seven bird, and two reptile species (Table 1). The number of species at any one nest site ranged from 1–6. For all 4 yr combined, mammals represented 72% of Red-tailed Hawk diet and birds represented 27% (Table 1). Only two reptile species were identified; they did not contribute greatly to the overall diet (<1%). Six species accounted for 67% of prey by frequency of occurrence: Nuttall's cottontail (*Sylvilagus nuttalli*, 17.6%), Kaibab squirrel (*Sciurus aberti kaibabensis*, 7.7%), rock squirrel (*Spermophilus variegatus grammurus*, 10.0%), golden-mantled ground squirrel (*S. lateralis lateralis*, 10.3%), Northern Flicker (*Colaptes auratus*, 10.7%), and Steller's Jay (*Cyanocitta stelleri*, 10.3%; Table 1). Rare occurrences of porcupine (*Erethizon dorsatum*), coyote (*Canis latrans*), and mule deer (*Odocoileus hemionus*) comprised <2% of overall Red-tailed Hawk diet.

Dissimilarity Measures and Niche Breadth. Prey species frequency identified from pellet and prey remains did not vary among years ($P = 0.3$), across habitat types ($P = 0.8$), or by collection technique ($P = 0.4$). Dietary niche breadth for Red-tailed Hawks pooled across nests for each year was 0.58 in 1998, 0.52 in 1999, 0.51 in 2000, and 0.65 in 2001. The mean and 95% confidence interval for Red-tailed Hawks niche breadth for all four years combined was 0.57 ± 0.11 . Calculated food niche breadths for Northern Goshawks for Arizona and several other western states did not fall within our confidence interval for Red-tailed Hawks (Table 2). Dietary overlap between the Red-tailed Hawk during this study and a Northern Goshawk diet from Boal's (1993) earlier study in the same area was 55% (number of common species/sum of species recorded for both raptors).

Table 1. Frequency of prey species in 140 samples (478 identified prey items) of pellets and prey remains collected from 42 Red-tailed Hawk nests, May–October 1998–2001, on the Kaibab Plateau, Arizona, U.S.A.

PREY SPECIES	FREQUENCY (N = 478)	PERCENT FREQUENCY	NEST OCCURRENCE (N = 42)	PERCENT NEST OCCURRENCE
Nuttall's cottontail (<i>Sylvilagus nuttallii</i>)	84	17.6	36	85.7
Golden-mantled ground squirrel (<i>Spermophilus lateralis</i>)	49	10.3	26	61.9
Rock squirrel (<i>Spermophilus variegatus grammurus</i>)	48	10.0	29	69.0
Kaibab squirrel (<i>Sciurus aberti kaibabensis</i>)	37	7.7	21	50.0
Chipmunk (<i>Eutamias</i> sp.)	27	5.6	20	47.6
Northern pocket gopher (<i>Thomomys talpoides</i>)	22	4.6	21	50.0
Long-tailed vole (<i>Microtus longicaudus</i>)	17	3.6	17	40.5
Red squirrel (<i>Tamiasciurus hudsonicus</i>)	15	3.1	13	31.0
Mouse (<i>Peromyscus</i> sp.)	13	2.7	9	21.4
Shrew (<i>Sorex</i> sp.)	11	2.3	10	23.8
Black-tailed jackrabbit (<i>Lepus californicus</i>)	8	1.7	8	19.0
Long-tailed weasel (<i>Mustela frenata arizonensi</i>)	5	1.0	5	11.9
Mule deer (<i>Odocoileus hemionus</i>)	5	1.0	5	11.9
Plains pocket mouse (<i>Perognathus flavescens</i>)	3	0.6	2	4.8
Porcupine (<i>Erethizon dorsatum</i>)	2	0.4	2	4.8
Ringtail (<i>Bassariscus astutus</i>)	1	0.2	1	2.4
Coyote (<i>Canis latrans</i>)	1	0.2	1	2.4
Northern Flicker (<i>Colaptes auratus</i>)	51	10.7	28	66.7
Steller's Jay (<i>Cyanocitta stelleri</i>)	49	10.3	26	61.9
Clark's Nutcracker (<i>Nucifraga columbiana</i>)	13	2.7	10	23.8
Unknown bird	8	1.7	7	16.7
Common Raven (<i>Corvus corax</i>)	3	0.6	3	7.1
Western Bluebird (<i>Sialia mexicana</i>)	1	0.2	1	2.4
Hairy Woodpecker (<i>Picoides villosus</i>)	1	0.2	1	2.4
Common Nighthawk (<i>Chordeiles minor</i>)	1	0.2	1	2.4
Unknown snake	3	0.6	2	4.8
Mountain short horned lizard ^a (<i>Phrynosoma douglassi</i>)	0	0.0	0	0.0

^a Mountain short horned lizard was positively identified as a prey species during observations, but was not found in the prey collections.

Table 2. Food niche breadth of nesting Northern Goshawks calculated from prey remains collected in Arizona and other western states.

LOCATION	NUMBER OF NESTS	FOOD NICHE BREADTH	SOURCE
Arizona	20	0.29	Boal and Mannan (1994)
California	114	0.41	Bloom et al. (1986)
New Mexico	8	0.36	Kennedy (1991)
Oregon	4	0.38	Reynolds and Meslow (1984)

DISCUSSION

Our results on the Kaibab Plateau were consistent with Red-tailed Hawks being feeding generalists and preying primarily upon rabbits (*Sylvilagus* spp.), black-tailed jackrabbits (*Lepus californicus*), and ground squirrels (*Spermophilus* spp; Preston and Beane 1993); however, Northern Flickers and Steller's Jays were also frequent in this diet analysis. Previous observation and prey remains analyses for Northern Goshawks on the plateau indicated goshawks also preyed mostly upon rabbits and hares, tree and ground squirrels, Northern Flickers, and Steller's Jays (Boal and Mannan 1994, Kaufmann et al. 1994, and Reynolds et al. 1994). Bosakowski and Smith (1992) found that in eastern forests, competition between accipiters and buteos is usually minimized by a difference in prey selection, with buteos typically having a higher proportion of mammals in their diet, and accipiters more avian prey.

Red-tailed Hawks frequently exhibit switching behavior, which is the capability to utilize whichever species is most abundant at the time (Steenhof and Kochert 1988). Predators that are generalists often have weak and variable prey preferences and will exhibit switching behavior, while specialists with strong or consistent preferences do not (Murdoch 1969). The wider niche breadth of Red-tailed Hawks on the Kaibab Plateau indicated weaker preferences compared to the narrower niche breadth of Northern Goshawks.

Red-tailed Hawks and Northern Goshawks frequently occupy similar nesting habitat on the Kaibab Plateau. Both species tend to nest in larger trees (\bar{x} DBH = 68.3–72.5 cm) and mid-slope in drainages (\bar{x} slope position = 0.36–0.37; LaSorte et al. 2004). Because they also nest in close proximity (<2000 m apart, USDA Forest Service, North Kaibab Ranger District unpubl. data), we suggest that they may also be utilizing the same foraging habitat. Unfortunately, pellets and prey remains do not

provide insight into any spatial or temporal partitioning of prey by these two species. However, our research clearly shows Red-tailed Hawks are preying upon many of the same species utilized by Northern Goshawks. Thus, we believe the potential for competition exists. We further hypothesize that the more generalist nature of Red-tailed Hawk diet and nesting habitat, in combination with the deterioration of late-successional forest habitat and concurrent creation of openings on the Kaibab Plateau, may tend to exacerbate any potential conflict. We suggest that additional research should be implemented to examine this potential competition, better quantify numbers of prey in both species' diets, and determine potential effects on such competition on Northern Goshawk management alternatives.

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