British Ecological Society

Dietary Responses of Three Raptor Species to Changing Prey Densities in a Natural Environment
Author(s): Karen Steenhof and Michael N. Kochert
Source: *Journal of Animal Ecology*, Vol. 57, No. 1 (Feb., 1988), pp. 37-48
Published by: British Ecological Society
Stable URL: http://www.jstor.org/stable/4761
Accessed: 07/05/2014 21:14

Your use of the JSTOR archive indicates your acceptance of the Terms & Conditions of Use, available at http://www.jstor.org/page/info/about/policies/terms.jsp

JSTOR is a not-for-profit service that helps scholars, researchers, and students discover, use, and build upon a wide range of content in a trusted digital archive. We use information technology and tools to increase productivity and facilitate new forms of scholarship. For more information about JSTOR, please contact support@jstor.org.

British Ecological Society is collaborating with JSTOR to digitize, preserve and extend access to *Journal of Animal Ecology.*

http://www.jstor.org

This content downloaded from 169.229.32.136 on Wed, 7 May 2014 21:14:16 PM
All use subject to JSTOR Terms and Conditions

Journal of Animal Ecology (1988), **57**, 37–48

DIETARY RESPONSES OF THREE RAPTOR SPECIES TO CHANGING PREY DENSITIES IN A NATURAL ENVIRONMENT

By KAREN STEENHOF and MICHAEL N. KOCHERT

Snake River Birds of Prey Research Project, Bureau of Land Management, 3948 Development Avenue, Boise, Idaho 83705 U.S.A.

SUMMARY

(1) Diets of three nesting raptor species were evaluated from 5939 prey items collected from nests in south-western Idaho during a 10-year period that included a complete jack rabbit population cycle and an unusual ground squirrel population crash.

(2) Jack rabbits were the principal prey of golden eagles; Townsend's ground squirrels were the main prey of prairie falcons and red-tailed hawks. Prairie falcons had the most specialized diets, and red-tailed hawks the most diverse. None of the three raptor diets reflected the relative abundance of prey types in the environment.

(3) Diet diversity of each of the three raptor species expanded as the abundance of their main prey declined. Ground squirrels and birds were alternate prey for eagles; gopher snakes, kangaroo rats, and rabbits were alternate prey for red-tailed hawks. Prairie falcons had no single important alternate prey species.

(4) Yearly frequencies of main prey in each of the three raptor diets were correlated with the annual abundance of that prey in the environment. Frequencies of alternate prey were correlated not with their own abundance but inversely with the abundance of the principal prey.

(5) Eagle preference for jack rabbits was strong and unaffected by changes in prey densities. Red-tailed hawk selectivity for jack rabbits was inversely related to ground squirrel abundance, suggesting 'switching' behaviour. Prairie falcon selectivity for ground squirrels did not vary with ground squirrel densities.

(6) Prey choice was generally consistent with predictions of the original optimal diet model, but red-tailed hawk prey selection appeared to depend on relative prey densities. Degree of diet specialization and plasticity are probably related to a raptor's life-history characteristics, and may influence a raptor's effects on its prey populations.

INTRODUCTION

Several investigations have documented dietary or functional responses of raptor breeding populations to changes in prey abundance (e.g. McInvaille & Keith 1974; Kellomaki 1977; Adamcik, Todd & Keith 1978, 1979; Goszczynski 1981; Nilsson 1981; Village 1981, 1982; Lindén & Wikman 1983; Korpimäki 1985). Few, however, have sought the possible mechanisms of prey selection.

From 1971 to 1981, prey densities, raptor densities, and raptor diets have been monitored in the 340 000 ha Snake River Birds of Prey Area (U.S. Department of Interior 1979). Each year, approximately 30 golden eagle (*Aquila chrysaetos*), 60 red-tailed hawk (*Buteo jamaicensis*), and 200 prairie falcon (*Falco mexicanus*) pairs nest in the Snake River

This content downloaded from 169.229.32.136 on Wed, 7 May 2014 21:14:16 PM
All use subject to JSTOR Terms and Conditions

Canyon (U.S. Department of Interior 1979). Populations of their prey species fluctuate. Black-tailed jack rabbit (*Lepus californicus*) abundance fluctuates cyclically (Gross, Stoddart & Wagner 1974), and Townsend's ground squirrel (*Spermophilus townsendii*) populations change in response to climatic conditions (Smith & Johnson 1985).

In this analysis, we examine the diets of three species of diurnal raptors nesting in the canyon to: (i) document their functional responses to changing prey densities; (ii) identify factors associated with diet specialization and plasticity; (iii) determine how raptor preferences for prey change in response to changing prey densities; and (iv) relate our findings to current theories about foraging strategies and predator–prey relationships.

MATERIALS AND METHODS

Study area

The study area is in south-western Idaho at 42°50′N, 115°50′W. Its principal physiographic feature is the Snake River Canyon, with basalt cliffs ranging from 2 to 125 m in height. Topography above the canyon is generally flat with a few isolated buttes. Elevation ranges from 770 m in the canyon bottom to 1000 m at the rim. Vegetation is characteristic of a shrub–steppe community, with big sagebrush (*Artemisia tridentata* Nutt.), shadscale (*Atriplex confertifolia* (Torr. & Frem.) Wats.) and winterfat (*Ceratoides lanata* (Pursh) J. T. Howell) vegetation associations.

Prey abundance

From 1977 through 1981, jack rabbit abundance was assessed by spotlighting from a vehicle along line transects (Smith & Nydegger 1985). In 1971, 1973, and 1975 through 1981 the average number of jack rabbits seen per day from late March through July by a two-person raptor survey crew was tabulated from field notes. Jack rabbits per crew-day and jack rabbit densities from spotlighting were correlated ($r = 0{\cdot}94$) from 1977 to 1981, and the relationship ($y = 0{\cdot}124 + 0{\cdot}099x$, where y = predicted density and x = jack rabbits per crew-day) was used to estimate pre-1977 jack rabbit densities. Jack rabbit density was highest in 1971, but it decreased sharply in 1973 and remained low through 1977 (Fig. 1). Numbers increased from 1978 through 1981, but the peak reached in 1981 was lower than that attained in 1971.

Townsend's ground squirrel densities were estimated from live-trapping grids from 1975 through 1981 (Smith & Johnson 1985). Hole count transects (U.S. Department of Interior 1979) were used to assess relative abundance of ground squirrels in different habitats. On the basis of subjective observations, we assumed that 1971 and 1973 ground squirrel densities were similar to those in 1975. Numbers of ground squirrels declined sharply in 1977 (Fig. 1) as a result of an unusually severe drought (Smith & Johnson 1985).

Abundances of other prey species were assessed each year from 1975 to 1978. Small rodents other than ground squirrels were censused using a combination of live-trapping and snap-trapping (U.S. Department of Interior 1979). Snake densities were assessed from captures in drift fences, and lizards were counted by observational strip census (Diller & Johnson 1982). Nuttall's cottontails (*Sylvilagus nuttallii*) were live-trapped in selected habitats, and passerines were censused along walking transects (U.S. Department of Interior 1979). Ring-necked pheasant (*Phasianus colchicus*) densities were estimated from crowing count surveys (Kimball 1949) and Idaho Fish and Game Department data (U.S. Department of Interior 1979). Because sampling methods detected no significant

This content downloaded from 169.229.32.136 on Wed, 7 May 2014 21:14:16 PM
All use subject to JSTOR Terms and Conditions

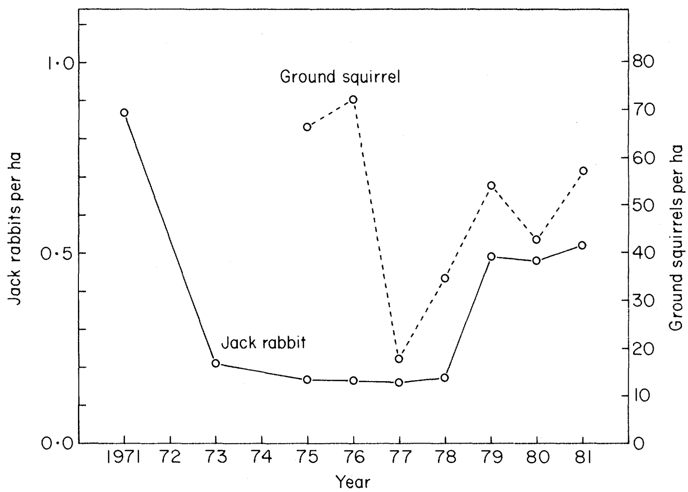

FIG. 1. Estimated density of black-tailed jack rabbits and Townsend's ground squirrels in the Snake River Birds of Prey Area, Idaho, U.S.A., 1971–81.

differences in populations of prey species other than jack rabbits and ground squirrels among years (1975–78), we used constant density values for all years of the study.

To account for variation in prey densities among habitats (Diller & Johnson 1982; Smith, Nydegger & Yensen 1984; Smith & Nydegger 1985; Nydegger & Smith 1986), we adjusted yearly estimates of prey density by considering habitat composition in generalized home ranges (Steenhof 1982) around nests where prey remains were collected. Based on relationships between prey density and habitats reported in U.S. Department of Interior (1979), we calculated annual prey densities as the average for all sample nests of a given raptor species, weighted by the number of collections made at each nest. However, because of the limited information on snake and cottontail distribution, we used average densities for the entire study area.

Raptor diets

Diets of the three raptor species were sampled by collecting prey remains and pellets from nests with young. Golden eagle nests were sampled in 1971 and from 1973 to 1981; red-tailed hawk nests from 1973 to 1980; and prairie falcon nests from 1974 to 1980. The number of nests sampled per species per year ranged from 4 to 17.

A 'collection' consisted of all prey remains and pellets gathered from a particular nest on one day. For quantitative comparisons of predation rates (number of prey per collection), we only used collections from nests where prey had accumulated for more than 3 days or less than 5 days. In all, 1294 collections were used in the analysis.

Prey items were identified and tabulated according to procedures described by Steenhof & Kochert (1985). Analyses were based on 5939 prey items; 2203 from golden eagles, 2065 from red-tailed hawks, and 1671 from prairie falcons. Prey collections from nests probably underestimated the total number of individuals taken but accurately reflected the relative frequencies of prey types in the diets (Collopy 1983a; Sitter 1983).

Weights were assigned to individual prey according to their sex and size class, based on average weights reported by Steenhof (1983). Prey weights were log-transformed and

This content downloaded from 169.229.32.136 on Wed, 7 May 2014 21:14:16 PM
All use subject to JSTOR Terms and Conditions

reported as 'geometric mean prey weights' (Sokal & Rohlf 1981; Jaksić & Braker 1983; Jaksić & Carothers 1985).

Population dietary breadth was calculated using Levins' (1968) formula:

$$B = \frac{1}{\sum_{i=1}^{n} P_i^2}$$

where P_i represents the proportion of the diet contributed by the ith taxon. Values of this index range from 1 to n. Breadth measures were based on the frequencies of individual prey species in the diet, as recommended by Greene & Jaksić (1983), except that woodrats (*Neotoma* spp.), kangaroo rats (*Dipodomys* spp.), dabbling ducks (*Anas* spp.), shrews (*Sorex* spp.), and gulls (*Larus* spp.) were grouped by genus, and invertebrates were grouped by order. Vertebrate prey that could not be identified to genus were excluded from calculations of diet breadth.

To assess the amount of variation among conspecific nesting pairs in a given year we used contingency tables to contrast the diets of each nesting pair sampled (Sherry 1984). A G-statistic (Sokal & Rohlf 1981) was calculated for each contingency table where the cases were nesting pairs and the classes were prey taxa. Individual prey species that comprised more than 10% of a raptor species' diet in any year were treated as separate classes; most other taxa were grouped by order. An index to 'population diet heterogeneity' (PDH) was computed by dividing the G-statistic by the degrees of freedom, where degrees of freedom equals the product: (prey taxa − 1) (pairs − 1) for the appropriate year and species (Sherry 1984).

Selectivity indexes were computed as:

$$S = (NE_1/NE_2 - N_1/N_2)/(NE_1/NE_2 + N_1/N_2),$$

where NE_i is the number of prey species i eaten per collection and N_i is the estimated density of species i in the environment (Jacobs 1974; Cock 1978).

RESULTS

General characteristics of raptor diets

Black-tailed jack rabbits were the main prey of golden eagles during the study period (Fig. 2a). Rodents, especially Townsend's ground squirrels, were the prey species found most frequently in red-tailed hawk and prairie falcon nests (Fig. 2b, and c). Red-tailed hawks had the most diverse diets of the three raptor species (diet breadth for all years pooled = 6·69). Red-tailed hawks consumed at least 69 different prey species between 1973 and 1980, three of which (Townsend's ground squirrel, Nuttall's cottontail, and gopher snake (*Pituophis melanoleucus* Daudin)) each comprised more than 10% of the prey items found at nests. Prairie falcons had the most specialized diets with a diet breadth of only 2·77. Although 64 different prey species were found in prairie falcon nests, the Townsend's ground squirrel was the only species that comprised more than 5% of the prey items found. Golden eagle diets were intermediate, with 65 prey species consumed and a diet breadth of 3·81. Two species, the jack rabbit and cottontail, each comprised more than 10% of the golden eagle prey items, and two others (ground squirrel and ring-necked pheasant) each comprised more than 5%.

This content downloaded from 169.229.32.136 on Wed, 7 May 2014 21:14:16 PM
All use subject to JSTOR Terms and Conditions

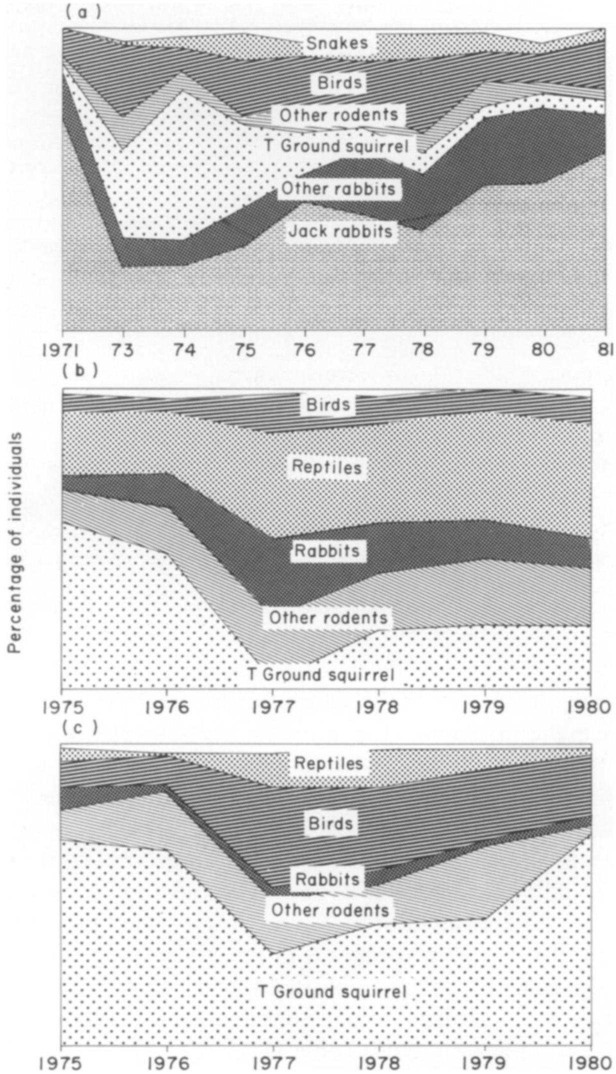

FIG. 2. Frequencies of major prey species in (a) golden eagle, (b) red-tailed hawk, and (c) prairie falcon diets.

Variation in diet among pairs within the population was lower for prairie falcons (PDH, $\bar{x}=1{\cdot}63$, $n=6$, S.D. $=0{\cdot}36$) than for golden eagles (PDH, $\bar{x}=2{\cdot}62$, $n=9$, S.D. $=0{\cdot}88$) or red-tailed hawks (PDH, $\bar{x}=2{\cdot}44$, $n=7$, S.D. $=0{\cdot}91$), emphasizing further the narrow food-niche of prairie falcons in the study area.

Geometric mean prey sizes were 690 g for eagles, 135 g for red-tailed hawks, and 97 g for prairie falcons. Sizes of prey taken ranged from 10 to 5800 g for eagles and from 1 to 2114 g for prairie falcons and red-tailed hawks. Golden eagles had the smallest variation in sizes of prey taken (coefficient of variation = 16%). Sizes of prey taken by red-tailed hawks were most variable (C.V. = 25%), and prairie falcons were intermediate (C.V. = 23%).

This content downloaded from 169.229.32.136 on Wed, 7 May 2014 21:14:16 PM
All use subject to JSTOR Terms and Conditions

TABLE 1. Raptor preference and avoidance of prey taxa for all years pooled, based on analytical methods described by Neu, Byers & Peek (1974). Significant ($P < 0{\cdot}05$) preference is indicated by +, avoidance by − and no preference or avoidance by N.S.

Prey species	Mean mass (g)*	Proportion of individuals in the environment†	Deviations of the diet from predicted frequencies in the environment: Golden eagle	Red-tailed hawk	Prairie falcon
Black-tailed jack rabbit	1512	(0·004–0·007)	+	+	N.S.
Nuttall's cottontail	536	(0·017–0·019)	+	+	N.S.‡
Townsend's ground squirrel	182	(0·041–0·121)	+‡	+	+
Snakes	174	(0·068–0·076)	−	+§	−
Other rodents	102	(0·677–0·734)	−	−	−
Passerines	81	(0·018–0·023)	NS‡	+§	+
Lizards	19	(0·081–0·108)	−	−	NS‡

* Based on weights reported by Steenhof (1983) and species and size class frequencies in the diets sampled for this analysis.

† Ranges given are based on mean yearly densities of prey at sample sites of each raptor species.

‡ A significant avoidance was exhibited when 'other rodents' were excluded from the analysis.

§ Preference was not significant when 'other rodents' were excluded from the analysis.

Frequencies of prey in each of the three raptor diets differed significantly from their relative abundance in the environment (χ^2 tests, 6 d.f., $P < 0{\cdot}01$; Table 1). Prey species that were the most common in the diets were not the most common in the environment. Golden eagles generally preferred the larger prey types and avoided the smallest prey. Red-tailed hawks also preferred the larger prey and, like eagles, avoided rodents other than ground squirrels. Prairie falcons concentrated on ground squirrels and passerines which were in the middle of the prey size range. Falcons showed neither preference nor avoidance for the largest and smallest prey, but they avoided both snakes and rodents other than ground squirrels. Several rodents in the study area were nocturnal and may therefore have been generally unavailable to diurnal raptors. Re-calculation of the preference patterns with nocturnal rodents excluded, however, showed only minor differences from the complete analysis (Table 1).

Yearly changes in diet composition

The proportion of the golden eagle diet comprised by jack rabbits fell from 72% in 1971 to 21% in 1973 as jack rabbit abundance declined (Fig. 2a). Associated with this decrease was a complementary increase in the percentage of rodents, birds, and other prey in the eagle diet. In 1973 and 1974, the percentage of Townsend's ground squirrels exceeded the percentage of jack rabbits in the diet. However, when jack rabbit populations increased after 1976, there was a concomitant increase in the proportion of the diet comprised by jack rabbits (Fig. 2a).

Ground squirrels were the principal prey of red-tailed hawks in 1975 and 1976, but they nearly disappeared from the red-tailed hawk diet in 1977, the year of lowest squirrel density (Fig. 2b). The proportions of several other prey species, notably gopher snakes, kangaroo rats (*Dipodomys* spp.), and rabbits increased in the red-tailed hawk diet during the years of low ground squirrel abundance. After 1977, the percentage of ground

This content downloaded from 169.229.32.136 on Wed, 7 May 2014 21:14:16 PM
All use subject to JSTOR Terms and Conditions

squirrels in the diet increased, but only to half of the level observed prior to the squirrel population crash. Rabbits, snakes, and other rodents continued to comprise substantial proportions of the red-tailed hawk diet in the last 2 years of the study.

Ground squirrels were the main prey of prairie falcons in all years. Although the percentage of ground squirrels in the diet declined during the drought year of 1977, squirrels still comprised more than 30% of prairie falcon prey in that year (Fig. 2c). There was no single important alternate prey species of prairie falcons during years of low ground squirrel abundance. Passerines as a group comprised 26% of the diet in 1977, but even the most commonly taken passerine (horned lark, *Eremophila alpestris* Linnaeus) never comprised more than 11% of the falcon diet in any single year. By 1980, ground squirrels had returned to pre-drought levels in the falcon diet.

Diet breadth and population diet heterogeneity

Diets of each raptor species expanded as populations of their main prey declined. Diet breadth of golden eagles was inversely correlated with jack rabbit density ($r=-0{\cdot}77$, $n=9$, $P<0{\cdot}01$) but not with squirrel or total prey density (Ps $>0{\cdot}18$). Red-tailed hawk diet breadth was inversely correlated with squirrel density ($r=-0{\cdot}85$, $n=6$, $P=0{\cdot}02$), total prey density ($r=-0{\cdot}77$, $n=6$, $P=0{\cdot}04$), and combined squirrel and rabbit densities ($r=-0{\cdot}83$, $n=6$, $P=0{\cdot}02$) but not with jack rabbit density ($P=0{\cdot}12$). Similarly, prairie falcon diet breadth was correlated with squirrel density ($r=-0{\cdot}83$, $n=6$, $P=0{\cdot}02$), total prey density ($r=-0{\cdot}78$, $n=6$, $P=0{\cdot}03$), and combined squirrel and jack rabbit densities ($r=-0{\cdot}84$, $n=6$, $P=0{\cdot}02$).

Population dietary breadth measures can be large if all or most nesting pairs in the population have a varied diet or if certain nesting pairs specialize in different prey items. Our index to specialization by pairs was population diet heterogeneity (PDH). Yearly PDH values did not correlate with either population diet breadth (Ps $>0{\cdot}16$) or prey densities (Ps $>0{\cdot}08$) in any of the three raptors, suggesting that most nesting pairs diversified their diets similarly during the prey shortage.

Numbers of individual prey per collection

Black-tailed jack rabbits were the only prey whose frequencies in the golden eagle diet correlated with their own densities in the environment (Table 2). The frequency of all other species except pheasants was inversely related to jack rabbit density, but not at statistically significant levels (Table 2; Ps $>0{\cdot}12$). Absolute densities of jack rabbits were slightly better predictors of prey frequencies in the eagle diet than were relative jack rabbit densities (Table 2).

Frequencies of alternate prey in the red-tailed hawk diet were also unrelated to their own abundance in the environment (Table 3). Instead, they were inversely related to the densities of the red-tailed hawk's main prey, ground squirrels. The inverse relationship with squirrel densities was significant ($P=0{\cdot}003$) for jack rabbit frequencies, and it approached significance for passerines and pheasants (Ps $=0{\cdot}06$ and $0{\cdot}11$, respectively). Ground squirrels were the only prey species whose frequencies in the diet were correlated with their own densities. However, relative squirrel densities were slightly better predictors of the red-tailed hawk diet than absolute densities (Table 3). None of the individual prey frequencies was correlated with jack rabbit densities (Ps $>0{\cdot}05$).

Frequencies of ground squirrels in the prairie falcon diet were positively and significantly correlated with squirrel densities and also combined ground squirrel/jack rabbit densities. Frequencies of three of the five alternate prey groups were inversely and

This content downloaded from 169.229.32.136 on Wed, 7 May 2014 21:14:16 PM
All use subject to JSTOR Terms and Conditions

TABLE 2. Correlation coefficients for prey densities in the environment and number of prey per collection in golden eagle diets, 1971–81 ($n=9$)

	Own density		Jack rabbit density	
	Absolute†	Relative‡	Absolute†	Relative‡
Black-tailed jack rabbit	0·73*	0·71*	0·73*	0·71*
Ring-necked pheasant	0·49	0·48	0·11	0·09
Townsend's ground squirrel	0·13	0·09	−0·44	−0·42
Other rodents	0·40	0·36	−0·42	−0·42
Passerines	−0·09	−0·25	−0·41	−0·41
Lizards	−0·20	−0·47	−0·23	−0·32

*$P<0{\cdot}05$.
† Actual density of prey in the environment.
‡ Fraction of the total prey density comprised by the taxa.

TABLE 3. Correlation coefficients for prey densities in the environment and number of prey per collection in red-tailed hawk diets, 1975–80 ($n=6$)

	Own density		Ground squirrel density	
	Absolute†	Relative‡	Absolute†	Relative‡
Black-tailed jack rabbit	0·02	0·07	−0·94*	−0·95*
Ring-necked pheasant	0·12	0·23	−0·58	−0·57
Townsend's ground squirrel	0·81*	0·84*	0·81*	0·84*
Other rodents	0·26	0·18	−0·22	−0·24
Passerines	−0·40	0·26	−0·71	−0·72
Lizards	0·36	0·30	0·36	0·36

*$P<0{\cdot}05$.
† Actual density of prey in the environment.
‡ Fraction of the total prey density comprised by the taxa.

significantly related to squirrel densities (Table 4). Absolute squirrel densities were better predictors of the frequencies of ground squirrels, lizards, and passerines in the diet, but relative squirrel numbers were slightly better predictors of pheasants (Table 4). The frequency of passerines in the falcon diet was positively and significantly correlated with relative passerine density ($P=0{\cdot}01$) but not with absolute passerine density. No other alternate prey taxa showed significant correlations between their own abundance and their frequency in the prairie falcon diet.

Selectivity indexes

Golden eagles showed a strong preference (mean selectivity for 9 years, $S=0{\cdot}92$) for jack rabbits over ground squirrels in all years of the study. Eagles also exhibited a preference for ground squirrels over the other prey combined ($S=0{\cdot}85$). Golden eagle selectivity for jack rabbits was unrelated to oscillations in either rabbit or squirrel numbers (Ps$>0{\cdot}23$).

Red-tailed hawks also preferred jack rabbits over ground squirrels (mean for 6 years, $S=0{\cdot}48$), but preference was not as strong as in eagles. Red-tailed hawks preferred ground squirrels over other prey species ($S=0{\cdot}84$). Selectivity for jack rabbits with respect to squirrels was inversely correlated with ground squirrel density ($r=0{\cdot}80$, $n=6$,

This content downloaded from 169.229.32.136 on Wed, 7 May 2014 21:14:16 PM
All use subject to JSTOR Terms and Conditions

TABLE 4. Correlation coefficients for prey densities in the environment and number of prey per collection in prairie falcon diets, 1975–80 ($n = 6$)

	Own density		Ground squirrel density	
	Absolute†	Relative‡	Absolute†	Relative‡
Black-tailed jack rabbit	−0·04	−0·09	0·35	0·36
Ring-necked pheasant	−0·25	−0·25	−0·79*	−0·85*
Townsend's ground squirrel	0·87*	0·85*	0·87*	0·85*
Other rodents	−0·53	−0·27	0·03	0·16
Passerines	−0·01	0·88*	−0·84*	−0·71
Lizards	−0·59	−0·23	−0·76*	−0·67

*$P < 0·05$.
† Actual density of prey in the environment.
‡ Fraction of the total prey density comprised by the taxa.

$P = 0·03$), but selectivity for ground squirrels over other prey was unaffected by variations in prey abundance.

Prairie falcons exhibited only a weak preference (mean for 6 years, $S = 0·18$) for ground squirrels over jack rabbits. In 2 of the 6 years, falcons actually preferred jack rabbits over squirrels, and in 1 year, there was no preference. Falcons, however, showed a strong preference ($S = 0·81$) for ground squirrels over other species. Selectivity for squirrels over rabbits was not correlated with the density of squirrels in the environment ($P = 0·44$), but it was positively correlated ($r = 0·97$, $n = 6$, $P < 0·01$) with jack rabbit density. Preference for squirrels over other prey was unaffected by changes in density of any prey species (Ps $> 0·31$).

DISCUSSION

Many theories attempt to identify the rules by which predators select prey. One of the most popular has been optimal foraging, the view that predators select prey to maximize fitness, usually net energy intake (MacArthur & Pianka 1966; Schoener 1971; Pulliam 1974; and reviews by Pyke, Pulliam & Charnov 1977; Krebs, Stephens & Sutherland 1983; Pyke 1984). In the original optimal diet model, predator preferences are based on profitabilities of prey and not relative frequencies of prey in the environment (Pulliam 1974). Other models attribute more importance to relative prey abundance, sometimes as a variation of existing optimal diet models (Hughes 1979; Glasser 1982, 1984a,b), otherwise as a separate theory (Murdoch & Oaten 1975; Fullick & Greenwood 1979; Greenwood & Elton 1979).

Schluter (1981) listed three predictions of the original optimal diet model for which there is little field evidence. First, when prey are abundant, predators should eat only the most valuable prey type. Second, inclusion of other prey types in the diet should depend not on their own abundance but on the abundance of more profitable prey. And finally, as prey abundance declines, diet diversity should increase.

The majority of our findings are consistent with these three predictions. None of the three raptor diets reflected the relative abundance of prey types in the environment. Instead, raptors exhibited consistent preferences for certain prey items and concentrated predation on a particular prey size range. Frequencies of alternate prey in the diet were related not to their own densities but inversely with the densities of the preferred prey. And finally, diets of all three raptor species expanded as prey densities, particularly of their main prey, declined.

This content downloaded from 169.229.32.136 on Wed, 7 May 2014 21:14:16 PM
All use subject to JSTOR Terms and Conditions

Data on red-tailed hawk diets may also support an alternative model of frequency-dependent prey selection. In contrast to eagles and falcons, red-tailed hawk selectivity for prey was affected by variations in prey density: selectivity for jack rabbits was inversely correlated with squirrel density, and relative prey densities were better predictors of the diet than absolute densities. Red-tailed hawks, therefore, showed evidence of 'switching' behaviour, preying disproportionately more on squirrels when they were abundant with respect to jack rabbits. Our results are consistent with Murdoch's (1969) finding that predators with weak but variable prey preferences exhibit switching behaviour while those with either strong preferences (eagles) or weak but consistent preferences (falcons) do not.

Differences in the raptors' degree of specialization can be explained by some of their life-history characteristics. Specialization is thought to be favoured when: (i) a predator exploits a stable and abundant food supply (Emlen 1968; Schoener 1971; Sherry 1984); (ii) the distance from the nest to the foraging area is great (Orians & Pearson 1979; Schoener 1979); (iii) predators rely more on pursuit than searching to secure their prey (MacArthur & Pianka 1966; Schoener 1971); and (iv) difference among prey values are large and unambiguous (Hughes 1979).

The generalist strategy of the red-tailed hawk is probably favoured because it is intermediate-sized, forages within a small, defended area around the nest (U.S. Department of Interior 1979), spends more time searching for rather than pursuing prey (Orde & Harrell 1977; Bildstein 1978), and probably encounters a wide variety of prey types and densities during its long migrations (Steenhof, Kochert & Moritsch 1984). Specialization may be favoured in the prairie falcon because of its extensive foraging ranges (U.S. Department of Interior 1979), its pursuit strategy of hunting (White 1962; Goslow 1971; Phipps 1979; Haak 1982), and the non-cyclic nature of its main prey. The golden eagle, with intermediate diet breadth and plasticity probably experiences pressures for both specialization and generalization. The eagle's relatively small foraging range (U.S. Department of Interior 1979), its searching rather than pursuit strategy of hunting (Collopy 1983b), and the cyclic nature of jack rabbit populations probably favour a wide food-niche, but year-round residency as well as year-round availability of jack rabbits may favour specialization. In addition, differences in prey profitabilities may be less ambiguous for the large eagle and small falcon than for the intermediate-sized red-tailed hawk.

Predator preferences and diet plasticity are factors that may significantly influence a raptor's effects on its prey populations (Hassell 1978). In our study the number of both the preferred and alternate prey taken by each raptor was strongly associated with density of the preferred prey. However, only in the generalist red-tailed hawk was the number of preferred prey taken related to the density of alternate prey. For predators like golden eagles and prairie falcons that have relatively fixed prey preferences, less preferred prey species apparently did not effectively 'buffer' predator rates on main prey.

Additional research is needed to determine: (i) if the preferred prey are in any way optimal for raptors, and (ii) if raptor predation affects prey population levels.

ACKNOWLEDGMENTS

This paper is a contribution from the U.S. Department of Interior, Bureau of Land Management's Snake River Birds of Prey Research Project. We are indebted to A. R. Bammann, J. H. Doremus, and numerous technicians who assisted in field data

This content downloaded from 169.229.32.136 on Wed, 7 May 2014 21:14:16 PM
All use subject to JSTOR Terms and Conditions

collection, and we thank the Idaho Cooperative Wildlife Research Unit for the 1971 golden eagle data. J. S. Whitman, L. Farley, R. M. Olson, and R. Haley analysed prey remains, and D. Ramirez tabulated much of the data. We thank F. M. Jaksić, C. R. Groves, and L. S. Young for valuable comments on draft manuscripts and T. E. Martin for discussions that helped shape many of the ideas presented.

REFERENCES

Adamcik, R. S., Todd, A. W. & Keith, L. B. (1978). Demographic and dietary responses of great horned owls during a snowshoe hare cycle. *Canadian Field-Naturalist*, **92,** 156–166.

Adamcik, R. S., Todd, A. W. & Keith, L. B. (1979). Demographic and dietary responses of red-tailed hawks during a snowshoe hare fluctuation. *Canadian Field-Naturalist*, **93,** 16–27.

Bildstein, K. L. (1978). Behavioral ecology of red-tailed hawks (Buteo jamaicensis), *rough-legged hawks* (B. lagopus), *northern harriers* (Circus cyaneus), *American kestrels* (Falco sparverius) *and other raptorial birds wintering in south central Ohio.* Unpublished Ph.D. thesis, Ohio State University.

Cock, M. J. W. (1978). The assessment of preference. *Journal of Animal Ecology*, **47,** 805–816.

Collopy, M. W. (1983a). A comparison of direct observations and collections of prey remains in determining the diet of golden eagles. *Journal of Wildlife Management*, **47,** 360–368.

Collopy, M. W. (1983b). Foraging behaviour and success of golden eagles. *Auk*, **100,** 747–749.

Diller, L. V. & Johnson, D. R. (1982). *Ecology of reptiles in the Snake River Birds of Prey Area.* U.S. Department of Interior, Bureau of Land Management, Boise, ID.

Emlen, J. T. (1968). Optimal choice in animals. *American Naturalist*, **102,** 385–389.

Fullick, T. G. & Greenwood, J. J. D. (1979). Frequency dependent food selection in relation to two models. *American Naturalist*, **113,** 762–765.

Glasser, J. W. (1982). A theory of trophic strategies: the evolution of facultative specialists. *American Naturalist*, **119,** 250–262.

Glasser, J. W. (1984a). Is conventional foraging theory optimal? *American Naturalist*, **124,** 900–905.

Glasser, J. W. (1984b). Evolution of efficiencies and strategies of resource exploitation. *Ecology*, **65,** 1570–1578.

Goslow, G. E. (1971). The attack and strike of some Northern American raptors. *Auk*, **88,** 815–827.

Goszczynski, J. (1981). Comparative analysis of food of owls in agrocenoses. *Ekologia Polska*, **29,** 431–439.

Greene, H. W. & Jaksić, F. M. (1983). Food-niche relationships among sympatric predators: effects of level of prey identification. *Oikos*, **40,** 151–154.

Greenwood, J. J. D. & Elton, R. A. (1979). Analysing experiments on frequency-dependent selection by predators. *Journal of Animal Ecology*, **48,** 721–737.

Gross, J. E., Stoddart, L. C. & Wagner, F. H. (1974). Demographic analysis of a northern Utah jackrabbit population. *Wildlife Monograph* 40.

Haak, B. A. (1982). *Foraging ecology of prairie falcons in northern California.* Unpublished M.S. thesis, Oregon State University, Corvallis.

Hassell, M. P. (1978). *The Dynamics of Arthropod Predator–Prey Systems.* Princeton University Press, Princeton, NJ.

Hughes, R. N. (1979). Optimal diets under the energy maximization premise: the effects of recognition time and learning. *American Naturalist*, **113,** 209–221.

Jacobs, J. (1974). Quantitative measurement of food selection: a modification of the forage ratio and Ivlev's electivity index. *Oecologia (Berlin)*, **14,** 413–417.

Jaksić, F. M. & Braker, H. E. (1983). Food-niche relationships and guild structure of diurnal birds of prey: competition versus opportunism. *Canadian Journal of Zoology*, **61,** 2230–2241.

Jaksić, F. M. & Carothers, J. H. (1985). Ecological, morphological, and bioenergetic correlates of hunting mode in hawks and owls. *Ornis Scandinavica*, **16,** 165–172.

Kellomaki, E. (1977). Food of the pygmy owl *Glaucidium passerinum* in the breeding season. *Ornis Fennica*, **54,** 1–29.

Kimball, J. W. (1949). The crowing count pheasant census. *Journal of Wildlife Management*, **13,** 101–120.

Korpimäki, E. (1985). Prey choice strategies of the kestrel *Falco tinnunculus* in relation to available small mammals and other Finnish birds of prey. *Annales Zoologici Fennici*, **22,** 91–104.

Krebs, J. R., Stephens, D. W. & Sutherland, W. J. (1983). Perspectives in optimal foraging. *Perspectives in Ornithology* (Ed. by A. H. Brush & G. A. Clark), pp. 165–216. Cambridge University Press, Cambridge.

Levins, R. (1968). *Evolution in Changing Environments.* Princeton University Press, Princeton, NJ.

Lindén, H. & Wikman, M. (1983). Goshawk predation on tetraonids: availability of prey and diet of the predator in the breeding season. *Journal of Animal Ecology*, **52,** 953–968.

MacArthur, R. H. & Pianka, E. R. (1966). On optimal use of a patchy environment. *American Naturalist*, **100,** 603–609.

This content downloaded from 169.229.32.136 on Wed, 7 May 2014 21:14:16 PM
All use subject to JSTOR Terms and Conditions

McInvaille, W. B., Jr & Keith, L. B. (1974). Predator–prey relations and breeding biology of the great horned owl and red-tailed hawk in Central Alberta. *Canadian Field-Naturalist*, **88,** 1–20.

Murdoch, W. W. (1969). Switching in general predators: experiments on predator specificity and stability of prey populations. *Ecological Monographs*, **39,** 335–54.

Murdoch, W. W. & Oaten, A. (1975). Predation and population stability. *Advances in Ecological Research*, **9,** 1–130.

Neu, C. W., Byers, C. R. & Peek, J. M. (1974). A technique of analysis of utilization-availability data. *Journal of Wildlife Management*, **38,** 541–545.

Nilsson, I. N. (1981). Seasonal changes in food of the long-eared owl in southern Sweden. *Ornis Scandinavica*, **12,** 216–223.

Nydegger, N. C. & Smith, G. W. (1986). Prey populations in relation to *Artemisia* vegetation types in southwestern Idaho. *Proceedings of the Symposium on the Biology of Artemisia and Chrysothamnus* (Ed. by E. D. McArthur & B. L. Welch), pp. 152–156. U.S. Department of Agriculture, Forest Service, Ogden, UT.

Orde, C. J. & Harrell, B. E. (1977). Hunting techniques and predatory efficiency of nesting red-tailed hawks. *Raptor Research*, **121,** 82–85.

Orians, G. H. & Pearson, N. E. (1979). On the theory of central place foraging. *Analysis of Ecological Systems* (Ed. by G. R. Stairs & R. D. Mitchell), pp. 155–177. Ohio State University Press, Columbus.

Phipps, K. B. (1979). *Hunting methods, habitat use and activity patterns of prairie falcons in the Snake River Birds of Prey Natural Area, Idaho*. Unpublished M.S. thesis, Western Illinois University, Macomb.

Pulliam, H. R. (1974). On the theory of optimal diets. *American Naturalist*, **108,** 59–74.

Pyke, G. H., Pulliam, H. R. & Charnov, E. L. (1977). Optimal foraging: a selective review of theory and tests. *Quarterly Review of Biology*, **52,** 137–154.

Pyke, G. H. (1984). Optimal foraging theory: a critical review. *Annual Review of Ecology and Systematics*, **15,** 523–575.

Schluter, D. (1981). Does the theory of optimal diets apply in complex environments? *American Naturalist*, **118,** 139–147.

Schoener, T. W. (1971). Theory of feeding strategies. *Annual Review of Ecology and Systematics*, **2,** 369–404.

Schoener, T. W. (1979). Generality of the size–distance relation in models of optimal feeding. *American Naturalist*, **114,** 902–914.

Sherry, T. W. (1984). Comparative dietary ecology of sympatric, insectivorous neotropical flycatchers (*Tyrannidae*). *Ecological Monographs*, **54,** 313–338.

Sitter, G. (1983). *Feeding activity and behavior of prairie falcons in the Snake River Birds of Prey Natural Area in southwestern Idaho*. Unpublished M.S. thesis, University of Idaho, Moscow, Idaho.

Smith, G. W. & Johnson, D. R. (1985). Demography of a Townsend ground squirrel population in southwestern Idaho. *Ecology*, **66,** 171–178.

Smith, G. W. & Nydegger, N. C. (1985). A spotlight line-transect method for surveying jack rabbits. *Journal of Wildlife Management*, **49,** 699–702.

Smith, G. W., Nydegger, N. C. & Yensen, D. L. (1984). Passerine bird densities in shrubsteppe vegetation. *Journal of Field Ornithology*, **55,** 261–264.

Sokal, R. R. & Rohlf, F. J. (1981). *Biometry*. W. H. Freeman, San Francisco.

Steenhof, K. (1982). Use of an automated geographic information system by the Snake River Birds of Prey Research Project. *Computers, Environment and Urban Systems*, **7,** 245–251.

Steenhof, K. (1983). Prey weights for computing percent biomass in raptor diets. *Raptor Research*, **17,** 15–27.

Steenhof, K. & Kochert, M. N. (1985). Dietary shifts of sympatric buteos during a prey decline. *Oecologia (Berlin)*, **66,** 6–16.

Steenhof, K., Kochert, M. N. & Moritsch, M. Q. (1984). Dispersal and migration of southwestern Idaho raptors. *Journal of Field Ornithology*, **55,** 356–368.

U.S. Department of Interior (1979). *Snake River Birds of Prey Special Research Report*. Bureau of Land Management, Boise, Idaho.

Village, A. (1981). The diet and breeding of long-eared owls in relation to vole numbers. *Bird Study*, **28,** 215–244.

Village, A. (1982). The diet of kestrels in relation to vole abundance. *Bird Study*, **29,** 129–138.

White, C. M. (1962). Prairie falcon displays Accipitrine and Circinnine hunting methods. *Condor*, **64,** 439–440.

(Received 3 September 1986)

This content downloaded from 169.229.32.136 on Wed, 7 May 2014 21:14:16 PM
All use subject to JSTOR Terms and Conditions