RELATIONSHIPS BETWEEN JACKRABBIT ABUNDANCE AND FERRUGINOUS HAWK REPRODUCTION

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ABSTRACT.—From 1966–70 and 1972–74, we studied relationships between Ferruginous Hawk (*Buteo regalis*) reproduction and abundance of their main prey, the black-tailed jackrabbit (*Lepus californicus*) in the eastern Great Basin Desert of central Utah. Correlation tests showed significant relationships between jackrabbit abundance and hawk reproduction: the population of nesting hawks, number of nesting pairs, total eggs laid and total young fledged varied in synchrony with jackrabbit abundance. Key Factor Analysis and stepwise removal procedures indicated that jackrabbit abundance influenced hawk reproduction in the following order of decreasing importance: number of nesting pairs; failure of nesting pairs to achieve maximum clutch size; total number of young fledged and total number of young hatched. Regression tests revealed that two of these, the failure to nest and achieve maximum clutch size, are important limiting factors on reproduction and at least partially act to regulate the size of this Ferruginous Hawk population.

Solomon (1949) proposed that predators respond to changing prey densities in two basic ways, functionally and numerically. In the functional response, a predator consumes prey of a given species at a rate according to the density of prey. In the numerical response, predator population density changes with changing prey density, usually through migration and/or corresponding adjustments in reproduction rate.

Studies of raptor responses to density changes of their main prey have been reviewed by Newton (1979). Important European investigations include those of Tawny Owls (*Strix aluco*) and their prey in England (Southern 1970), Goshawk (*Accipiter gentilis*) clutch sizes and game bird abundance in Finland (Sulkava 1964), and Common Buzzard (*Buteo buteo*) breeding sequences relative to vole densities in Norway (Hagan 1969). In North America, Rusch et al. (1972) examined Great Horned Owl (*Bubo virginianus*) reproduction responses to snowshoe hares (*Lepus americanus*) near Alberta, while Hamerstrom (1979) reported Marsh Hawk (*Circus cyaneus*) breeding responses to vole (*Microtus pennsylvanicus*) abundance in Wisconsin. In this study, we analyze the numerical response of Ferruginous Hawk (*Buteo regalis*) reproduction to changes in its main prey, the black-tailed jackrabbit (*Lepus californicus*).

The Ferruginous Hawk is the largest and most powerful of North American buteos and is the most common nesting raptor in the eastern Great Basin Desert of Utah. The black-tailed jackrabbit is a characteristic and frequently abundant mammal in the same area. It fluctuates in abundance, possibly cyclically, over a period of several years (Gross et al. 1974). The jackrabbit is an important prey species in the diet of the Ferruginous Hawk, comprising in some years more than 85–90% of the total food biomass (Smith and Murphy 1973, 1978, 1979; Howard and Wolfe 1976; Woffinden and Murphy 1977).

STUDY AREA

D.G.S. studied relationships between Ferruginous Hawks and jackrabbits on an 1,170 km² portion of the eastern Great Basin Desert in central Utah. The area includes Rush and Cedar valleys in Utah and Tooele counties. Woffinden and Murphy (1977) selected a 932 km² section of the original study area for their investigation. Topographically, the area is characterized by broad, flat, alkaline valleys separated by high, north-south oriented hills and ranges. Valley elevations range from 1,460 to 1,620 m and maximum elevations range from 1,830 m to 2,440 m.

Climatically, the area is a northern cold desert. Annual precipitation averages 38 cm and monthly temperatures average from −5°C in January to 24°C in July, with wide daily and seasonal variations.

Two distinct vegetative associations are present. The desert shrub community occurs over the lower elevations and covers the valley floors. It consists of shrubs, herbs, and grasses, several of which form large, homogeneous stands under certain edaphic soil conditions. Predominant desert shrub species include big sagebrush (*Artemisia tridentata*) on the better-drained

TABLE 1.   Ferruginous Hawk reproduction, 1967–70, 1972–74.[1]

	1967	1968	1969	1970	1972	1973	1974
No. pairs	19	31	38	20	20	11.3	8.6
No. nesting pairs	15	28	34	13	18.8	8.8	3.6
Eggs producible[2]	73.2	119.4	146.3	77	77	43.5	33.1
Total eggs produced	36	104	129	35	50.6	18.8	10
Eggs/nest	2.5	3.7	3.8	2.9	2.7	2.1	2.4
Eggs producible[3] (breeding pairs)	57.8	107.8	130.9	50.1	72.4	33.9	13.9
Eggs hatched	15	60	99	17	38.8	15	8.8
Young/nest	1.3	2.4	3.1	1.0	2.7	2.1	2.4
Young fledged	12	55	90	10	38.8	6.3	3.8
Young fledged/nest	1.2	2.2	2.9	1.4	1.9	0.7	1.0
Jackrabbit index in Rush-Cedar valleys	3.3	9.03	13.8	3.6	—	3.2	1.8

[1] Data from 1972–74 are weighted to compensate for the reduced study area size.
[2] Eggs producible with all pairs breeding and achieving maximum observed clutch size of 3.8 in 1969.
[3] Eggs producible with actual pairs breeding and achieving maximum observed clutch size of 3.8 in 1969.

soils, and greasewood (*Sarcobatus vermiculatus*) on the poorly drained valley floors. The well-drained slopes and hills support a dwarf conifer community of Utah juniper (*Juniperus osteosperma*) and pinyon pine (*Pinus monophylla*), which occur in stands of widely varying density.

METHODS

D.G.S. investigated Ferruginous Hawk-jackrabbit relationships from 1966–70, and N.D.W. and J.R.M. from 1972–74. Search methods for hawk pairs and breeding activity were similar in both periods. The study area was subdivided into 2.56-km² units, which were systematically searched in a rotating sequence. Foot searches of cliffs, rock outcrops and juniper stands were supplemented by vehicle searches through desert shrub. Fixed-wing aircraft surveys were used two years to find nests but were of limited use due to minimum speed and altitude requirements. Observations of courtship, territorial, and hunting behaviors were useful in establishing presence and status of pairs. Fieldwork each year was from December through August. During this time, D.G.S. spent a minimum of two days per week on the study area, and total field work per year averaged 1,640 hours. Status and productivity of all pairs and nests were checked at weekly intervals or shorter throughout the breeding season. We believe that all pairs and nests were located and monitored each year because of a combination of factors including: the open and accessible habitat, conspicuousness of the birds during territorial and hunting activities, conspicuousness of the bulky nests, and continuing sequence of the survey throughout the study months.

From 1966–70, D.G.S. determined jackrabbit abundance by transect counts. Permanent linear transects, each 805 m long, were marked off through six large desert shrub communities selected at random in the study area. Counts on all six transects were taken every two weeks from mid-December through March by two persons spaced 20 m apart. Results for each year were pooled to obtain an index of jackrabbit abundance.

Woffinden and Murphy (1977) used five randomly distributed square transects 0.25 m on a side to determine jackrabbit abundance each year.

The relationship between yearly jackrabbit abundance and Ferruginous Hawk reproduction may be considered in terms of specific phases of the breeding sequence: (1) number of pairs present, (2) number of pairs nesting, (3) average clutch sizes, (4) total egg production, (5) average brood size and (6) total number of young fledged.

We used correlation analysis to examine the variation between each of these reproduction phases and yearly jackrabbit abundance. To determine if observed variations in the reproduction phases were correlated with jackrabbit abundance or resulted from covariance with other phases, we used procedures described by Smith (1973), which are briefly reiterated herein. Hawk reproduction data were first transformed by Key Factor Analysis (KFA), which provides a ranking of the failure to achieve maximum fecundity, hatching success and fledging success. Using KFA terminology, each of these phases are considered separate mortalities which may be compared with the total mortality (K) occurring during reproduction.

We confined our KFA to reproduction mortalities as follows:

k_1 = log (total pairs × maximum clutch) − log (laying pairs × maximum clutch). Largest number of pairs and average clutch size was 38 pairs and 3.8 eggs in 1969.

k_2 = log (total laying pairs × maximum clutch) − log (total laying pairs × eggs actually produced).

k_3 = log (eggs laid) − log (eggs hatched).

k_4 = log (eggs hatched) − log (young fledged).

$K = k_1 + k_2 + k_3 + k_4$.

To determine the contribution and relationship of the mortalities at each breeding stage (k_i) to the total mortality during hawk reproduction (K), a variance-covariance matrix was generated for the four k-values and total K. Inspection of the matrix reveals the most important k-value, which is the one having the highest covariance with K. The contribution of the remaining k-values and residual K is assessed by stepwise removal of all k-values in order of importance (from R. H. Smith 1973):

residual killing power, $K' = K - k_p = \sum_{i=1}^{n} k_i$ $(i \neq p)$

We tested significance of each mortality-contributing k-factor by regression of the k-values against untransformed hawk population densities.

RESULTS AND DISCUSSION

JACKRABBIT ABUNDANCE

Indices of jackrabbit abundance determined from transect counts in the Rush and Cedar valleys study areas in central Utah are presented in Table 1. The yearly index

is the average of all transect counts taken from December through March of each year. Rush-Cedar valleys indices for 1967–70 were determined by D. G. Smith (1973) and for 1972–74 by Woffinden and Murphy (1977). The indices in Table 1 show the jackrabbit highs and lows and magnitude of the observed fluctuations during the seven-year study. Jackrabbit populations in Rush and Cedar valleys increased from 1967 through 1969, declined in 1970 and again dropped from 1973–74.

HAWK REPRODUCTION

Yearly data on Ferruginous Hawk nesting populations and reproduction are presented in Table 1. The correlation between jackrabbit densities and number of hawk pairs is significant (r = 0.95; t = 6.00; $P < 0.01$). Nesting populations in the low jackrabbit years, 1973 and 1974, were but 22.6% and 29.7%, respectively, of the Ferruginous Hawk population in spring, 1969, the peak year of jackrabbit abundance. The observed recruitment illustrates the first component of numerical response by this migratory raptor. Galushin (1974), Phelan and Robertson (1978), Hamerstrom (1979) and others have documented the ability of migratory or nomadic species to concentrate rapidly in areas of prey abundance.

The second numerical response component includes all habits directed towards increasing reproduction, beginning with the percentage of pairs that attempted to nest. We considered pairs to be breeding if a nest was constructed and attended. The number of nesting pairs was significantly correlated (r = 0.96; t = 6.99; $P < 0.01$) with the density of jackrabbits. The percentage of total pairs nesting varied from a high of 89.0% in 1969 to a low of 42.0% in 1974. The tendency of pairs to nest in high prey years and refrain from breeding in low prey years has been documented for several raptor species (Pitelka et al. 1955, Rusch et al. 1972, Hamerstrom 1979, and others). Southern (1970) found that Tawny Owls commonly react to a scarcity of prey by fewer pairs nesting.

Average clutch size and number of young fledged, but not average brood size, varied with jackrabbit abundance. Average clutch sizes varied from a high of 3.8 in 1969, the peak jackrabbit year, to 2.1 in 1973, a low jackrabbit year. Similarly, average number of young fledged per nest was highest (2.9) in 1969 and lowest (0.7 and 1.0) in the low jackrabbit years of 1973 and 1974. Average brood size was highest in 1969 but did not vary in synchrony during years of medium

and low jackrabbit abundance, suggesting that incubation success of Ferruginous Hawks may decline with larger clutches. The total number of eggs produced, young brooded, and young fledged showed similar significant correlations with jackrabbit densities (r = 0.99; $P < 0.01$ for each). The resulting production of fledglings in high prey years was over 15 times the total number produced in the year of lowest jackrabbit density. Extremes in total production of young also have been noted in other raptor species. Production of young by Snowy Owls (*Nyctea scandiaca*) near Barrow, Alaska (Pitelka et al. 1955) and the Wytham Wood population of Tawny Owls (Southern 1970) were highest during years when rodents were most abundant and decreased in synchrony with decreasing rodent abundance. Both species produced no young during the year when prey were scarcest. In Wisconsin, Hamerstrom (1979) found a greater than three-fold difference in production of young Marsh Hawks between years of low and high vole numbers.

All factors contributing to the second component of numerical response, from increased percentage of nesting pairs through total number of young fledged are probably interrelated in sequential fashion. Density of prey probably affects both the stimulus and the physiological ability to breed, and influences whether or not a pair of Ferruginous Hawks will nest in a particular year. Prey density also affects the health of the female and may limit the number of eggs laid. The amount of time the adults require for foraging, both to supply themselves and their young, also depends on prey density. As prey becomes scarcer, adults must spend more time foraging and less time caring for eggs and young. This decreased care may reduce the number of young produced in a given year.

KEY FACTOR ANALYSIS OF RELATIONSHIPS BETWEEN JACKRABBIT ABUNDANCE— HAWK REPRODUCTION

The demonstrated synchrony of jackrabbit abundance and aspects of Ferruginous Hawk reproduction suggests that jackrabbits as food represent an important limiting factor on hawk reproduction. As jackrabbits become more plentiful, the breeding population and productivity of hawks increases. Conversely, scarcity of jackrabbits appears to deter breeding and increase the probability of failure to achieve maximum fecundity and lowered success in at least some of the breeding phases.

TABLE 2. Estimated k-values for the four stages of mortality and total K.*

k-value	1967	1968	1969	1970	1972	1973	1974	Mean
k_1	0.309	0.061	0.047	0.343	0.183	0.365	0.510	0.259
k_2	0.206	0.001	0.000	0.156	0.056	0.256	0.430	0.159
k_3	0.380	0.240	0.121	0.314	0.116	0.098	0.055	0.189
k_4	0.097	0.038	0.042	0.230	0.000	0.377	0.365	0.164
K	0.992	0.350	0.210	1.043	0.355	1.096	1.360	0.772

* Stages defined in methods section.

KFA transformation of the reproductive data is presented in Table 2 and the variance-covariance matrix of the transformed data is presented in Table 3. The latter reveals that k_1, the failure of pairs to nest, constitutes the greatest loss of Ferruginous Hawk reproduction. Territorial fidelity of non-nesting pairs differed according to abundance of prey. In years when prey were scarce, pairs usually deserted a territory very early in the breeding season, whereas when prey were plentiful, at least some non-nesting pairs were seen on the territories throughout most of the spring and early summer. Southern (1970) also found that the failure to nest was the most important factor in limiting Tawny Owl reproduction. Unlike the more nomadic Ferruginous Hawks, pairs of Tawny Owls remained on the territories even during years of lowest prey abundance (Southern 1970).

Removal of k_1 (Table 4) reveals that k_2, the failure of nesting pairs to achieve maximum clutch size, was the next most important reproduction-limiting factor. Average clutches in 1968 and 1969, when prey were abundant, were significantly greater than in 1967 and 1974, when prey were scarce (t = 2.56, 2.81, respectively; $P < 0.05$ for both), but not significantly different from each other (t = 0.07, t = 1.3 for high and low prey years respectively; $P < 0.05$ for both). The k_2 loss of production strongly reinforces k_1 and shows high covariance with it. Together, factors k_1 and k_2 caused most of the loss of productivity.

Factor k_4, the loss due to failure of young to fledge, was the third most important source of mortality. This factor also shows high covariance with k_1 and k_2. Factor k_3, the failure of eggs to hatch, varied inversely with factors k_1, k_2, and k_4, and may act in compensatory fashion.

Southern (1970), Ito (1972), R. H. Smith (1973) and others suggested that the directed, density-dependent mortality of each k_1 factor may be determined by regression of k-values against untransformed population numbers. Our regression of k-values against untransformed Ferruginous Hawk numbers indicates that two of the four causes of lowered reproduction were density-dependent.

The least squares estimate of k_1, the loss in production due to failure of pairs to breed, is:

$$k_1 = 0.455 - 0.004 \quad (N_1).$$

The regression is significant (t = 3.21; $P < 0.05$), and accounts for 88% of the total variation in k_1. The estimate of k_2, the failure of pairs to achieve maximum clutch size, is:

$$k_2 = 0.319 - 0.003 \quad (N_2).$$

The regression of N_2 on k_2 is also significant (t = 3.22; $P < 0.05$) and accounts for 71.9% of the variation in k_2.

Neither k_3, hatching success, nor k_4, fledging success, was a significant density-dependent factor in lowering production ($P > 0.05$ for both), although k_4 acts in a weakly density-dependent mode. From his KFA of Tawny Owl reproduction, Southern (1970) suggested that three factors, k_1 (failure to nest), k_2 (failure to achieve maximum clutch size) and k_5 (overwinter loss) contributed the greatest mortality to total generation loss. R. H. Smith (1973) reanalyzed Southern's data and found that only over-

TABLE 3. Variance-covariance for the four k-values and the total K.

k-value	k_1	k_2	k_3	k_4	K
k_1	0.0290				
k_2	0.0252	0.0238			
k_3	−0.0022	−0.0043	0.0151		
k_4	0.0231	0.0211	−0.0062	0.0254	
K	0.0750	0.0658	0.0025	0.0634	0.2067

TABLE 4. Covariances of k-values and residual K after stepwise removal of k-values.

k-value removed	k_1	k_2	k_3	k_4	K
1	0.0750	0.0658	0.0025	0.0634	0.2067
2	—	0.0406	0.0047	0.0403	0.0857
4	—	—	0.0090	0.0192	0.0282
3	—	—	0.0151	—	0.0152

winter loss was significantly density-dependent. Reproduction and population densities of Ferruginous Hawks are undoubtedly regulated by additional factors not considered in this report, such as postfledging loss and overwinter disappearance.

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