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Some physical and biological factors affecting red-tailed hawk productivity

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Various physical and biological factors affecting annual productivity in a Red-tailed Hawk population in north-central Oregon were investigated. The percentage of the population successfully fledging one or more young was the most important factor in determining the number of young fledged per pair in a given year. Neither clutch size

nor the number of young fledged per successful nest varied significantly. Percent pair success was correlated with several January weather variables. A cold and dry January is positively correlated with Red-tailed Hawk productivity. This is apparently related to the onset of rapid vegetative growth, and this in turn is positively correlated with the timing of the emergence and reproductive cycle of the principal prey, Belding's and Townsend's ground squirrels, (Turner 1972). Because a cold and dry January delays the emergence of ground squirrels, the period of emergence and dispersal of the young squirrels more closely corresponds to the time of peak food needs of the young Red-tailed Hawks, and greater pair success is observed. This relative abundance of prey appears to be of greater importance than actual abundance.

Red-tailed Hawk productivity was found to correlate significantly with two habitat variables: the presence of adequate numbers of dispersed hunting perches and relative ground squirrel abundance. The presence of one or more perches per sixteenth section provided the best single correlation. Neither territory size nor competition from interspecifically territorial Swainson's Hawks were correlated with productivity of Red-tailed Hawk territories. Red-tailed Hawks with inhabited dwellings within their territories fledged significantly more young than those without.

SOME PHYSICAL AND BIOLOGICAL FACTORS AFFECTING

RED-TAILED HAWK PRODUCTIVITY

by

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CHAPTER I

INTRODUCTION

Productivity, the number of young fledged per pair or territory per breeding season, varies significantly in many avian populations. Both annual and interpair variation have been observed and have been attibuted to a number of factors. Review papers pertaining to clutch sise and certain other aspects of productivity are presented by Lack (1947, 1948), Klomp (1970), and Hussell (1972).

Little work has been conducted on variation in productivity of raptors. Because raptors are relatively long-lived species, they have the evolutionary option of varying reproductive effort more than short-lived passerines. This flexibility can present a greater source of variation in productivity and may permit a closer correlation of productivity with the prevailing environmental conditions. Raptors also occupy a position high on the food chain. If raptors are energy-limited, their position would make them comparatively sensitive to variability in their food supply. Therefore, energetic factors influencing productivity may be more easily discerned. The few studies that have investigated this problem in detail within a raptor population include Cave (1968) with the Kestrel (Falco tinnunculus) and Southern (1970) with the Tawny Owl (Strix aluco).

Significant annual variation in raptor productivity has been noted in several studies (Cave 1968; Fitch et al., 1946; Houston 1975;

Lack 1947, 1948; McInvaille and Keith 1974; Mebs 1964; Pitelka et al., 1955; Schmaus 1938; Southern 1970; Tubbs 1967; USDI 1979). In contrast, other studies have found no apparent variation (Picozzi and Wier 1974; Smith and Murphy 1973). Several factors, particularly food abundance, appear to be important. Food abundance has been observed to operate at various stages in the reproductive cycle. It has been correlated with non-breeding (Houston 1975; Pitelka et al. 1955; Southern 1970), clutch size (Cave 1968; Houston 1975; Lack 1947, 1948; McInvaille and Keith 1974; Mebs 1964; Schmaus 1938; Southern 1970), nest desertion (Cave 1968; Southern 1970), and loss of young (Lack 1947, 1948; Mebs 1964; Schmaus 1938; Southern 1970). Weather has been correlated with productivity, but except for the study of McInvaille and Keith (1974) in which nestlings were killed directly by inclement weather, this relationship has been only indirectly related to productivity through the impairment of the hunting ability of the parents (Cave 1968; Southern 1959, 1970). Annual variations in productivity have also been ascribed to population density (Cave 1968), laying date (Cave 1968), and predation (Fitch et al., 1946; Hagar 1957; McInvaille and Keith 1974).

Variations in interpair productivity have been less studied. Southern (1970) inferred that the age of the birds - at least of the male, which does most of the hunting - may be correlated with productivity. The time of laying (Cave 1968), habitat at a general level (Southern 1970; Olendorff and Stoddart 1974; Picozzi and Wier 1974), and competition through density (Southern 1970) have also been correlated with territory productivity.

It is the intent of this work to investigate various physical and biological factors affecting both annual and interterritorial productivity in a Red-tailed Hawk population. Factors studied include structural and biological habitat features, weather, and competition. Red-tailed Hawks were chosen for this study as they are easily observed and territories are easily delimited. Predation, density, and laying date - potentially complicating sources of variability in productivity - were not found to vary in this population, permitting more direct study of the factors in question.

CHAPTER II

METHODS

The study area covers 124 square kilometers in the shrub-steppe region of north-central Oregon. The site encompasses a broad valley with rolling hills and is drained by three small creeks. Rimrock-lined canyons are found in some areas. Elevations range from 677-1308m. The land is used primarily for the grazing of cattle and dryland farming of wheat. The natural vegetation is characteristic of the Columbia Basin province as described by Franklin and Dyrness (1973). The dominant associations include big sage (Artemisia tridentata)/bluebunch wheatgrass (Agropyron spicatum) and bluebunch wheatgrass/Idaho fescue (Festucca idahoensis). A long history of grazing, however, has reduced the abundance of the perennial grasses, and such species as cheatgrass (Bromus tectorum) and gray rabbitbrush (Chrysothamnus nauseosus) are now ubiquitous. Junipers (Juniperus occidentalis) are the only trees of any abundance on the area and are locally common. Black poplars (Populus nigra) and black locusts (Robina pseudo-acacia) are found around many of the dwellings including abandoned homesteads.

The study was conducted from 1973 through 1979 with most of the field work conducted from March through June each year. During this time Red-tailed Hawks were observed in order to detetermine density, territorial boundaries, reproductive outcome, and behavior associated with territoriality and the reproductive effort.

Territory is defined as the area defended by or regularly occupied by a pair. This definition is similar to the definition of "utilized territory" of Odum and Kuenzler (1955). A "regularly occupied" area is defined as an area for which there is more than one observation. This definition includes areas for which no active defense was noted (resulting for the most part from a lack of intruders). Pairs existed that shared no boundary with another Buteo, and whose area, therefore, could not be considered defended.

All observations were recorded on field maps as a flight line and/or perching. Date, time, individual, and incidence of territorial defense were noted. These field maps were then compiled to delimit territory boundaries. Territories were then used as they existed after the arrival of the Swainson's Hawk (Buteo swainsoni) for the following analyses. Territorial boundaries were most accurately determined in 1977 and 1978 and were the ones used.

Though Red-tailed Hawks are comparatively tolerant of nest visits by investigators after the young have hatched (personal observation; Luttich et al., 1971), disturbance was kept to a minimum when determining productivity. A single visit to the nest vicinity was made, if necessary, when the young were between three and four weeks old. At this age young do not attempt to flee the nest nor are they likely to be deserted by the parents. Young present at this time were assumed to survive until fledging. This is based on my experience that no mortality other than attributable to man has been observed among nestlings between three weeks of age and fledging in any of the approximately 50 nests followed through fledging on or adjacent to the study area. Age of the young was estimated, and any prey remains were noted at this time. Laying date was calculated assuming a 32-day incubation period (Luttich et al., 1971). If the nest was undefended, it was examined to note any evidence of eggs or young that would aid in determining the time and cause of failure.

Several measures of productivity are used in this paper. One is annual productivity. This is defined as the number of young fledged per pair per breeding season. Those pairs whose reproductive outcome was altered directly by human activity are either eliminated, if disturbed prior to the young reaching three weeks of age, or considered fledged if older. Other measures relating to annual productivity include percent pair success, young fledged per success, and clutch size. A pair was considered successful if it fledged one or more young. Little information was gained regarding average clutch size because of the caution exercised in the nest vicinity. A measure was attempted using unhatched eggs found plus young observed. The resulting measure of clutch size is necessarily a minimum because of the potential disappearance of eggs or young prior to the nest visit.

Another productivity measure was that of territory productivity. This figure is the average productivity for a given territory during the period of the study. Territories are used as opposed to pairs, as not all territories were occupied continuously. Territory occupancy is as much a part of the measure of a territory's quality as the number of young fledged. However, because of the incomplete data for many of the territories and the great variance in annual productivity, a compensating figure was needed. Territory productivity was measured by subtracting the annual average territory productivity for a given year from an individual territory's productivity. This is done for each year there is data for a territory. An average is then calculated from the resulting differences. This average difference is the average number of young fledged above or below the seven-year average. The corrected territory productivity is this difference added to the seven-year average territory productivity.

Food habits were determined from observed captures and by prey remains found at the nest site. Prey weights were determined from specimens captured on the study area, museum specimens, and the literature.

Climatological data used to test the possible effects of weather upon Red-tailed Hawk productivity were obtained from the National Oceanic and Atmospheric Administration (NOAA) Antelope 1N station. The Antelope 1N station (moved in late 1978 1.6km south) is the only NOAA station located on the study area. Variables derived from these data were selected for their potential relationships to both direct and indirect effects upon Red-tailed Hawk annual productivity. The direct effects upon the Red-tailed Hawk include the period of egg-laying and incubation. Three kinds of variables pertain to indirect effects: (1) previous growing season effects upon the principal prey species, (2) summer weather effects on the onset of estivation of the principal prey species, and (3) fall and winter effects on vegetative growth and emergence from hibernation of the principal prey species. The variables are self-explanatory except for 174 degree date. It was developed as a potentially better temperature variable in predicting vegetative growth than January temperature. The variable, 174 degree date, is the day from January 1 each year where the summed daily degrees above freezing reached 174. It is figured as follows:

$$174 \text{ degree date} = d$$

when

$$\sum_{d=1}^{365} (\bar{x}_d - 32) \quad 174. \quad \text{If } \bar{x}_d < 32, \text{ then } \bar{x}_d - 32 = 0$$

where: d = the day of the year from January 1

$\bar{x}_d$ = the average temperature of day d in °F.

The number 174 was selected by using half the maximum reached by the first eight weeks of the warmest year. Ground squirrels have emerged from hibernation by the end of February even in the coldest of winters.

All variables were tested against annual productivity and its component parts through simple linear regression and step-wise multiple linear regression. Annual productivity and its component parts were first tested for significant annual variation by one-way analysis of variance. Component parts of annual productivity were also tested against annual productivity by means of correlation. The level of significance for all tests here and following is set at the 95% confidence interval.

Habitat composition was determined by dividing the study area into 768 sixteenth sections based on township and section boundaries. Parameters measured within each sixteenth section include the number of junipers in each of three height classes (<2m, 2-5m, <5m), the number of utility poles and poplars, the dominant plant species, topography, and the presence or absence of the following: Belding's ground squirrels (Spermophilus beldingi), Townsend's ground squirrels (Spermophilus townsendii), springs, streams, inhabited dwellings, and cliffs. Topography was measured by counting the number of contour lines crossed by a circle inscribed within each sixteenth section. USGS topographic maps were used with a contour interval of 6.1m. In addition to noting the presence of Belding's and Townsend's ground squirrels, abundance was rated on a scale of one to five based on the number observed and the area covered by the colony within the sixteenth section.

For each Red-tailed Hawk territory, the sixteenth sections that most closely conformed to the actual territory boundaries were used to derive habitat measures. The variables selected pertain to suitability for Red-tailed Hawk foraging, prey presence and abundance, nest sites, and human presence.

Variables affecting suitability of a territory for foraging include hunting perches, topography, and vegetative structure. A number of variables involving density and dispersion of hunting perches and topography were derived to test the importance of these features. Perches were defined as junipers greater than 2m tall, utility poles, and poplars. Topography was assessed using both the average and percentage of a territory (sixteenth sections) with greater than 61m (ten contour lines) elevational difference. The measures involving dispersion were derived as follows. A sixteenth section was considered adequate for efficient foraging under several conditions involving minimum perch densities. The minimum densities include one, three, five, seven, and ten perches. Other measures, adding the presence of cliffs and elevational differences, were developed. For example, a sixteenth section was considered huntable if it contained either the required number of perches or either a cliff or an elevational difference equal to or greater than 61m.

Vegetative structure was also tested with respect to Red-tailed Hawk territory productivity. A high density of shrubs or trees could potentially interfere with the observation and capture of prey. The percentage of a territory that was dominated by shrub or tree species was tested against territory productivity.

Several variables regarding prey presence and abundance were tested. These include the number of sixteenth sections with either Belding's or Townsend's ground squirrel colonies or both, the relative abundance of ground squirrels, the amount of surface water, and the abundance of wheat.

The availability of nest sites was also tested against territory productivity. Junipers greater than 5m tall, poplars, and cliffs were considered potential nest sites. Utility poles, though used as nest sites, were not considered as they are inferior to other nest sites and produce significantly less young (Janes, unpublished data). To test the effect of continual human presence on Red-tailed Hawk productivity, territories were separated into two classes: those with inhabited dwellings and those without.

The statistical tests used with respect to the above included both simple linear regression and step-wise multiple linear regression. To test the relationship involving human presence, the t-test was used. Only the 22 territories with three or more years of productivity data were used in the analyses. All figures in percentage form were arcsine converted.

Interpair competition among Red-tailed Hawks was tested on the basis of territory size. Territory size was determined by cutting and weighing territory representations traced from the territory maps. The method of determining territory boundaries is described above. These results were then tested against territory productivity by simple linear regression.

The effects of interspecies competition were also tested. Upon determination that Red-tailed Hawks and Swainson's Hawks were interspecifically territorial, Red-tailed Hawk territories were divided into two groups: those with contended boundaries and those with none. Differences in the territory productivity means for each group were then tested by the t-test.

CHAPTER III

RESULTS

The major portion or all of 31 Red-tailed Hawk territories existed on the study area. The rate of occupancy for these territories was 96% (n = 152). Other diurnal raptors occupying the study area included Swainson's Hawks (16 pairs), Golden Eagles (*Aquila chrysaetos*, 2 pairs), Prairie Falcons (*Falco mexicanus*, 3 pairs), and American Kestrels (*Falco sparverius*, approximately 35 pairs).

Red-tailed Hawks in the valley are migratory. A few birds (less than 10% of the breeding population) winter in the valley, but it is unknown whether these are a part of the breeding population. Band returns from Oregon Red-tailed Hawks have come from as far away as central Mexico (USDI, personal communication). The hawks arrive on the area over a short period of time usually during the second week in March. Almost immediately upon arrival they establish territories. Territory boundaries change very little from year to year with few exceptions and are maintained by the pairs throughout their stay on the area. Judging from the many individuals recognized by their distinctive plumage, there is very faithful return to previously held territories. Territories are strongly defended. Defense depends on many factors including weather, time of day, behavior of the intruder, and behavior and condition of the proprietor. Hunting areas, perches, and the nest vicinity are most actively defended.

The period of egg-laying and the initiation of incubation occur during the last week of March and the first few days of April. The average date for the initiation of incubation for the five years with adequate data is April 1. The average for each year has fallen within two days of this date. Extreme dates for individual pairs are March 17 and April 16.

Summaries of both territory and annual productivity and its component parts (Tables I and II) are based on data adjusted for human disturbance. Human influence had a relatively minor effect upon Red-tailed Hawk productivity. Only five cases of disturbance were noted out of 114 nesting attempts (4%) involving three pairs. Three cases apparently involved people taking young; the other two involving workers pushing nests with eggs off utility poles. No cases of predation were observed on any nest. No cases of nest desertion could be attributed to investigator disturbance.

Belding's ground squirrels comprised the greatest portion of the food taken both in terms of individuals and biomass (Table III). The importance of Belding's and Townsend's ground squirrels is probably underestimated as most of the food data originated from pairs with below average numbers of these species in their territories. Of the 31 pairs of Red-tailed Hawks, all but one had either a Belding's or a Townsend's ground squirrel colony on their territory. Twenty-six (84%) have Belding's ground squirrels, and ten pairs (34%) have Townsend's ground squirrels. Prey species of secondary importance include mountain cottontails (*Sylvilagus nuttallii*) and northern pocket gophers (*Thomomys talpoides*).

TABLE I

SUMMARY OF RED-TAILED HAWK TERRITORY PRODUCTIVITY
MISSING FIGURES ARE YEARS WITHOUT DATA
PARENTHESES INDICATE THAT THE
TERRITORY WAS UNOCCUPIED

Pair	1973	1974	1975	1976	1977	1978	1979	$\bar{x}$	Adjusted $\bar{x}$
Highlander						0		.00	.67
Hasting	2	2	2	2	2	2	2	2.00	2.00
PPL			0		2	1	2	1.25	1.57
Weasel							3	3.00	3.02
Four Hils				0	2	0		.67	.99
Grub Hollow	0	0	0	(0)	0	2		.33	.29
Scrag			0					.00	.77
Armstrong	*	2*	0	0	0	0	0	.33	.50
Antelope	4	4*	3	*	2	*	1	2.80	2.55
Windsock					3			3.00	2.85
Kaber				2		0	3	1.67	2.05
Max				3	2	0	2	1.75	1.98
Watershed	2	0	0	(0)	2	(0)	0	.57	.57
Savannah						0	0	.00	.34
Boar Coon							2	2.00	2.02
Lone Poplar						0	0	.00	.34
Ashburn	3	3		0	(0)	0	2	1.33	1.21
Horse Harness			0	0	2	2	2	1.20	1.55
Muddy Crossroads		2	0	2	2	3	3	2.00	2.17
Cold Camp Creek			0	2	3	0	3	1.60	1.89
Lazuli			0		0	0	0	.00	.32
Homestead			0			0	0	.00	.48
Van Guilder					2	0	0	.67	.84
Badger Bin		2		0	2	3	3	2.00	2.04
Eagle Valley Gate			1	0				.50	1.10
Pine Ridge					1	(0)	(0)	.33	.50
Kali						0	0	.00	.33
King Canyon						2	2	2.00	2.34
Foreman	3	3		3	0	0	0	1.50	1.50
Borthwick	3	3	0	0	2	2	2	1.71	1.71
Snowstorm	2		3				2	2.33	2.26
Young/territory	2.38	2.10	.60	.93	1.53	.71	1.36	1.37	
n	8	10	15	15	19	21	25		

* Figures were compensated for human disturbance (see text).

TABLE II

RED-TAILED HAWK ANNUAL PRODUCTIVITY MEASURES FOR 1973-1979
FIGURE IN PARENTHESES INDICATE SAMPLE SIZE

Measure	1973	1974	1975	1976	1977	1978	1979	$\bar{x}$
% pair success	88.8 (8)	80.0 (10)	26.7 (15)	46.2 (13)	76.2 (19)	36.4 (22)	62.5 (24)	54.3
Clutch size	2.71 (7)	2.63 (8)	2.14 (9)	2.50 (8)	2.33 (18)	2.10 (10)	2.31 (16)	2.39
Young fledged/success	2.71 (7)	2.63 (8)	2.25 (4)	2.33 (6)	2.07 (14)	2.13 (8)	2.27 (15)	2.34
Annual productivity*	2.38 (8)	2.10 (10)	.60 (15)	1.08 (13)	1.53 (19)	.77 (22)	1.42 (24)	1.41

* Young fledged/pair

TABLE III

RED-TAILED HAWK FOOD HABITS DETERMINED FROM PREY REMAINS FOUND AT THE NEST SITE AND PREY OBSERVED CAPTURED

Species	Indv.	Indv.	Indv. Biomass (g)	Total Biomass (g)	% Biomass
Spermophilus beldingi Belding's ground squirrel	15	34.1	243[1]	3645	48.9
Spermophilus townsendii Townsend's ground squirrel	3	6.8	166[2]	498	6.7
Sylvilagus nuttallii mountain cottontail	3	6.8	433[2]	1299	17.4
Thomomys talpoides northern pocket gopher	7	15.9	70[3]	490	6.6
Microtus montanus montane vole	3	6.8	30[2]	90	1.2
Peromyscus maniculatus deer mouse	2	4.5	22[3]	44	.6
Total Mammal	33	75.0		6066	81.3
Coluber constrictor common racer	2	4.5	77[2]	154	2.1
unidentified snake	4	9.1	207[2]	828	11.1
Total Reptile	6	13.6		982	13.2
Pica pica black-billed magpie	1	2.3	170[2]	170	2.3
Sturnella neglecta western meadowlark	1	2.3	96[2]	96	1.3
Eremophila alpestris horned lark	1	2.3	26[2]	26	.3
unidentified bird	2	4.5	60[3]	120	1.6
Total Bird	5	11.4		412	5.5
Total	44	100.0		7460	100.0

1 Portland State University collection
2 USDI (1979)
3 This study

Although percent pair success, clutch size, and young fledged per success were significantly correlated with annual productivity, percent pair success was the best predictor of annual productivity. Percent pair success alone contributed to 95% ($p < .01$) of the variability. Clutch size and young fledged per success accounted for 77% ($p < .01$) and 59% ($p < .05$) respectively of the variability in annual productivity. However, neither clutch size nor young fledged per success varied significantly from year to year.

No weather variables were found that significantly correlated with annual productivity (Table IV), but percent pair success was significantly correlated with January precipitation (Table V). However, the winter of 1978-1979, especially the month of January, was unusually severe. A January temperature 14.4°F below average is expected about once every 161 years ($p < .0062$). Thus, it may be more instructive to look at the results from the six previous years, omitting 1979 in reference to January variables (Table VI). The results in this case show significant correlations between annual productivity and both 174 degree date and January average temperature. Percent pair success is significantly correlated with four January related variables: 174 degree date, January average temperature, January precipitation, and January through April precipitation.

All weather variables significantly correlated with annual productivity or percent pair success involve the period of the onset of rapid vegetative growth of the year in question. No correlations were found with the previous growing season, previous summer weather, or weather potentially affecting Red-tailed Hawk incubation and egg-lay-

TABLE IV

SIMPLE LINEAR REGRESSION ANALYSES OF RED-TAILED HAWK ANNUAL PRODUCTIVITY TO WEATHER CORRELATIONS FOR 1973-1979

Variable	r^2	Slope
Direct Effects		
March precipitation	.004	-.092
March average temperature	.008	.021
April precipitation	.289	-.472
April average maximum temperature	.279	.073
Previous Growing Season		
January precipitation	.330	.567
January average temperature	.028	.035
January-April precipitation	.060	.101
January-April average temperature	.008	.053
April-May precipitation	.067	-.165
April-May average temperature	.217	.166
174 degree date	.065	.021
Previous Summer		
June-July precipitation	.073	.231
July precipitation	.016	-.157
July average temperature	.321	.320
Immediate Growing Season		
September-January precipitation	.000	.000
September-April precipitation	.102	-1.54
January precipitation	.502	-.814
January-April precipitation	.350	.217
January-April average temperature	.000	.000
174 degree date	.279	.028

* $p < .05$
** $p < .01$

TABLE V

SIMPLE LINEAR REGRESSION ANALYSES OF RED-TAILED HAWK PERCENT PAIR SUCCESS TO WEATHER CORRELATIONS FOR 1973-1979. Y-INTERCEPT PROVIDED IF A CORRELATION IS SIGNIFICANT

Variable	r^2	Slope	Y-intercept
Direct Effects			
March precipitation	.024	-5.81	
March average temperature	.006	.500	
April precipitation	.368	-14.2	
April average maximum temperature	.480	2.55	
Previous Growing Season			
January precipitation	.383	16.4	
January average temperature	.093	1.70	
January-April precipitation	.085	3.19	
January-April average temperature	.015	1.99	
April-May precipitation	.050	-3.84	
April-May average temperature	.195	4.21	
174 degree date	.026	.347	
Previous Summer			
June-July precipitation	.076	6.32	
July precipitation	.018	-4.54	
July average temperature	.253	7.60	
Immediate Growing Season			
September-January precipitation	.018	-.806	
September-April precipitation	.029	-.031	
January precipitation	.644*	-24.7	67.1
January average temperature	.155	-1.01	
January-April precipitation	.472	-6.73	
January-April average temperature	.008	.723	
174 degree date	.335	.811	

* $p<.05$
** $p<.01$

TABLE VI

SIMPLE LINEAR REGRESSION ANALYSES OF RED-TAILED HAWK ANNUAL PRODUCTIVITY AND PERCENT PAIR SUCCESS TO WEATHER CORRELATIONS FOR 1973-1978 Y-INTERCEPT PROVIDED IF A CORRELATION IS SIGNIFICANT

Variable	r^2	Slope	Y-intercept
Annual Productivity			
January precipitation	.547	-.885	
January average temperature	.688*	-.174	7.14
January-April precipitation	.537	-.331	
174 degree date	.703*	.070	-1.19
Percent Pair Success			
January precipitation	.702*	-26.8	68.0
January average temperature	.718*	-4.76	194.
January-April precipitation	.726*	-10.3	76.0
174 degree date	.841**	2.06	-37.9

* $p < .05$
** $p < .01$

ing. No combination of variables significantly added to the amount of variation answered by the above variables alone.

Results of habitat correlates to territory productivity tests are presented in Table VII except those pertaining to human presence. Only two parameters were found to be significant in the absence of others. These include percentage of a territory with one or more perches per sixteenth section and percentage of a territory with one or more perches or a cliff per sixteenth section. Other measures of perch dispersion incorporating greater perch densities were insignificant. However, in combination with relative ground squirrel abundance all perch dispersion measures were significant (Table VIII). Relative ground squirrel abundance was not significant by itself. The best predictor of territory productivity was a combination of percentage of a territory with one or more perches or a cliff per sixteenth section and relative ground squirrel abundance. Other parameters did not contribute significantly to these results. Territory size also had no observable effect upon productivity.

Territory productivity was positively and significantly correlated to the presence of inhabited dwellings. Pairs with inhabited dwellings fledged on the average 1.75 young per pair while those without inhabited dwellings fledged only 1.11 young per pair ($p < .01$).

Red-tailed Hawks and Swainson's Hawks were strongly interspecifically territorial. Swainson's Hawks arrive on the study area between April 4 and 15. The range of individual plumage variation between Swainson's Hawks in the Antelope area and their behavior permit identification of individuals with some confidence, and Swainson's Hawks

TABLE VII

SIMPLE LINEAR REGRESSION ANALYSES OF RED-TAILED HAWK TERRITORY PRODUCTIVITY TO HABITAT CORRELATIONS. Y-INTERCEPT PROVIDED IF A CORRELATION IS SIGNIFICANT

Variable	r^2	Slope	Y-intercept
Juniper density greater than 2m	.097	.015	
Perch density	.120	.016	
% of territory with 1 or more perches	.346**	.021	.169
% of territory with 3 or more perches	.176	.012	
% of territory with 5 or more perches	.178	.012	
% of territory with 7 or more perches	.099	.011	
% of territory with 10 or more perches	.106	.011	
% of territory with 1 or more perches or a cliff	.342**	.022	.137
% of territory with 3 or more perches or a cliff	.179	.012	
% of territory with 5 or more perches or a cliff	.150	.011	
% of territory with 7 or more perches or a cliff	.073	.009	
% of territory with 10 or more perches or a cliff	.087	.010	
% of territory with 3 or more perches or a cliff or more than 61m elevation difference	.085	.009	
% of territory with 5 or more perches or a cliff or more than 61m elevation difference	.069	.008	
% of territory with 7 or more perches or a cliff or more than 61m elevation difference	.013	.004	
% of territory with 10 or more perches or a cliff or more then 61m elevation difference	.020	.005	
Belding's ground squirrel colonies	.029	.043	
Ground squirrel colonies	.004	.020	
Relative ground squirrel abundance	.149	.053	
Average topography	.062	-.083	
% of territory with more than 61m elevation difference	.109	-.070	
Cliffs	.095	-.269	
Streams	.010	-.027	
Surface water	.059	-.065	
% of territory in shrubs	.099	.013	
% of territory in herbs	.040	-.009	
% of territory in wheat	.032	-.010	
Potential nest sites	.044	.002	
Territory size	.000	.000	

* $p < .05$
** $p < .01$

TABLE VIII

STEP-WISE MULTIPLE LINEAR REGRESSION ANALYSES OF RED-TAILED HAWK TERRITORY PRODUCTIVITY TO HABITAT RELATIONSHIPS. THE SLOPES ARE FOR VARIABLES IN THE EQUATION AFTER THE LAST SIGNIFICANT VARIABLE HAS BEEN ENTERED

Step Variable	r^2	Significance of multiple regression	Significance of variable	Slope
1 Relative ground squirrel abundance	.149	n.s.*	<.05	.064
2 Density of junipers >2m	.301	<.05	<.05	.019
3 % of territory in wheat	.313	n.s.	n.s.	-
(Y-intercept)				(.501)
1 Relative ground squirrel abundance	.149	n.s.	<.05	.062
2 Perch density	.315	<.05	<.05	.019
3 % of territory in wheat	.321	n.s.	n.s.	-
(Y-intercept)				(.476)
1 % of territory with 1 or more perches	.346	<.01	<.01	.021
2 Relative ground squirrel abundance	.482	<.01	<.05	.051
3 % of territory in wheat	-	n.s.	n.s.	-
(Y-intercept)				(-.275)
1 % of territory with 3 or more perches	.176	n.s.	<.01	.015
2 Relative ground squirrel abundance	.409	<.01	<.01	.069
3 % of territory in wheat	.410	<.05	n.s.	-
(Y-intercept)				(.082)
1 % of territory with 5 or more perches	.176	n.s.	<.01	.016
2 Relative ground squirrel abundance	.436	<.01	<.01	.073
3 % of territory in wheat	.438	<.05	n.s.	-
(Y-intercept)				(.099)
1 Relative ground squirrel abundance	.149	n.s.	<.01	.069
2 % of territory with 7 or more perches	.328	<.05	<.05	.015
3 % of territory in wheat	.338	n.s.	n.s.	-
(Y-intercept)				(.285)
1 Relative ground squirrel abundance	.149	n.s.	<.01	.069
2 % of territory with 10 or more perches	.337	<.05	<.05	.016
3 % of territory in wheat	.342	n.s.	n.s.	-
(Y-intercept)				(.381)
1 % of territory with 1 or more perches or a cliff	.342	<.01	<.01	.022
2 Relative ground squirrel abundance	.483	<.01	<.05	.054
3 % of territory in wheat	.493	<.01	n.s.	-
(Y-intercept)				(-.358)

TABLE VIII (Cont.)

Step	Variable	r^2	Significance of multiple regression	Significance of variable	Slope
1	% of territory with 3 or more perches or a cliff	.179	n.s.	<.01	.016
2	Relative ground squirrel abundance	.429	<.01	<.01	.071
3	% of territory in wheat	-	n.s.	n.s.	-
	(Y-intercept)				(003)
1	% of territory with 5 or more perches or a cliff	.150	n.s.	<.01	.016
2	Relative ground squirrel abundance	.436	<.01	<.01	.078
3	% of territory in wheat	.437	<.05	n.s.	-
	(Y-intercept)				(.013)
1	Relative ground squirrel abundance	.149	n.s.	<.01	.073
2	% of territory with 7 or more perches or a cliff	.319	<.05	<.05	.015
3	% of territory in wheat	.330	n.s.	n.s.	-
	(Y-intercept)				(.231)
1	Relative ground squirrel abundance	.149	n.s.	<.01	.073
2	% of territory with 10 or more perches or a cliff	.337	<.05	<.05	.016
3	% of territory in wheat	.342	n.s.	n.s.	-
	(Y-intercept)				(.309)
1	Relative ground squirrel abundance	.149	n.s.	<.01	.090
2	% of territory with 3 or more perches or a cliff or more than 61m elevation difference	.423	<.01	<.01	.018
3	% of territory in wheat	.431	<.05	n.s.	-
	(Y-intercept)				(-.508)
1	Relative ground squirrel abundance	.149	n.s.	<.01	.095
2	% of territory with 5 or more perches or a cliff or more than 61m elevation difference	.423	<.01	<.01	.019
3	% of territory in wheat	.426	<.05	n.s.	-
	(Y-intercept)				(-.448)
1	Relative ground squirrel abundance	.149	n.s.	<.01	.087
2	% of territory with 7 of more perches or a cliff or more than 61m elevation difference	.294	<.05	<.05	.015
3	% of territory in wheat	.299	n.s.	n.s.	-
	(Y-intercept)				(-.112)
1	Relative ground squirrel abundance	.149	n.s.	<.01	.088
2	% of territory with 10 or more perches or a cliff or more than 61m elevation difference	.311	<.05	<.05	.015
3	% of territory in wheat	.316	n.s.	n.s.	-
	(Y-intercept)				(-.047)

* n.s. not significant

appear to be as faithful to territories as Red-tailed Hawks. Usually within 24 hours of their arrival, Swainson's Hawks have established territorial boundaries conforming quite closely to those of the previous year. If adjacent Red-tailed Hawks have incorporated what becomes Swainson's Hawk territory into their own, the resulting confrontation can be impressive. The aerial combat between the two pairs can be very aggressive and last almost the entire first day. The males are involved in most of the aggression, and the female Red-tailed Hawk, which is normally incubating, participates little. By the second day the contesting of territorial boundaries drops off sharply though the resulting territorial boundaries are defended upon intrusion throughout the breeding season. Though Red-tailed Hawks may lose territory to Swainson's Hawks, this occurs only at the periphery of the Red-tailed Hawk's range, and the resulting boundaries look very similar to those of the previous year. No significant difference in productivity was found between Red-tailed Hawk pairs contending with Swainson's Hawks and those that did not.

CHAPTER IV

DISCUSSION

The principal factor determining annual productivity is the percentage of pairs that are able to successfully fledge young. Neither clutch size nor survival of nestlings appear to be significant. All significant correlations between percent pair success and various weather parameters involve January of the immediate year. If some event in January is responsible for percent pair success, it rules out direct effects upon the Red-tailed Hawk since they winter to the south. This suggests that the significant factor has something to do with the onset of the immediate growing season, most likely the availability of prey.

The emergence of the principal prey, the Belding's ground squirrel, from hibernation varies from year to year (Costain 1977; Morton and Sherman 1978; Turner 1972). In the Sierra's of California emergence has been observed to vary as much as six weeks (Morton and Sherman 1978). This is at least loosely correlated with weather and more directly related to the appearance of sufficient forage (Costain 1977; Morton and Sherman 1978; Turner 1972). Belding's ground squirrels in Oregon have been observed to emerge anytime from the third week in January to April (Costain 1977) and possibly even June (Turner 1972) depending on the location and elevation. Antelope is near the lower elevation range of the Belding's ground squirrel, and the squirrels emerge quite early. Backdating from the emergence of young and from observations of landowners, the Antelope populations at least occasionally emerge as early as late January and as late as the end of February.

The reproductive cycle in the Belding's ground squirrel is timed from the point of emergence from hibernation (Turner 1972). Therefore, in a year where the beginning of rapid vegetative growth begins earlier, the Belding's ground squirrel would be expected to emerge earlier. By emerging earlier, this would advance their reproductive cycle.

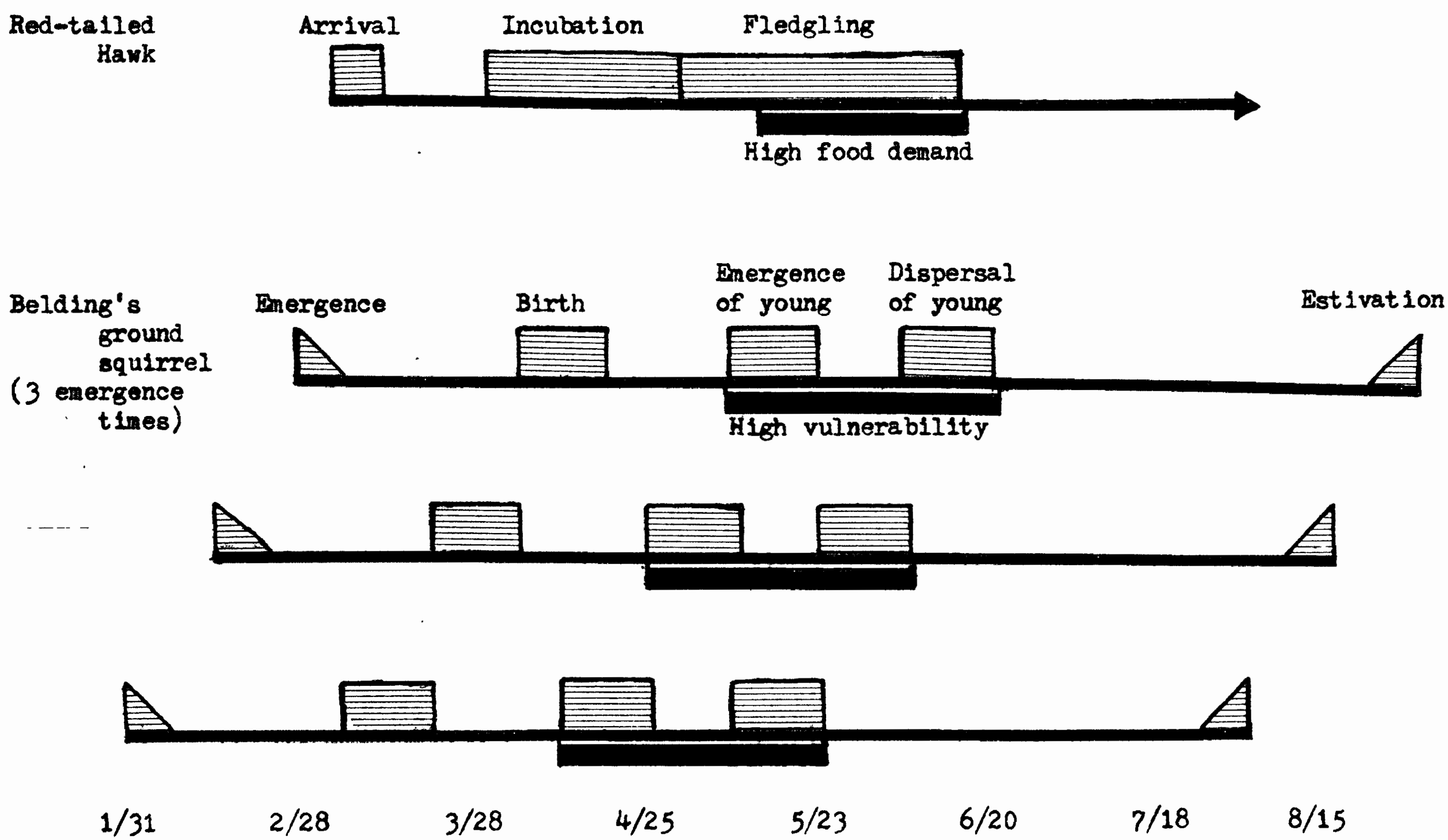
The question now becomes one of explaining what conditions lead to the beginning of rapid vegetative growth. The principal forage for Belding's ground squirrels is succulent vegetation (Costain 1977; Turner 1972). In the Antelope area this is most commonly winter annuals, primarily cheatgrass, or the perennial alfalfa. Winter annuals in general and cheatgrass in particular germinate with the beginning of the fall rains in September and October (Harris 1967). During the fall most of the growth is directed to the developing root system (Harris 1967). With the onset of cold weather, growth slows (Harris 1967). Warming late in the winter and early spring triggers rapid vegetative growth (Harris 1967). Cheatgrass is also sensitive to precipitation, and growth is limited by dry, cold spring weather (Harris 1967). In the Antelope area the beginning of rapid vegetative growth begins in late January or February. Alfalfa, too, begins vegetative growth with the onset of warmer weather. Therefore, a cold, dry January would be expected to delay the emergence of Belding's ground squirrels. This also helps explain why 174 degree date is more closely related to Red-tailed Hawk productivity than January average temperature. Plants presumably only grow appreciably when the temperature is above freezing. In this respect January average temperature is not the best measure of growing conditions. A day averaging 0°F and one of 20°F may be the same to the plants in terms of growth. Also, the period of January does not necessarily emcompass the entire period of importance.

To relate this to Red-tailed Hawk productivity, it is necessary to examine their reproductive chronology and compare it to that of the Belding's ground squirrel (Figure 1). The date of the initiation of incubation does not appear to vary significantly. Therefore, the relative timing of breeding between Red-tailed Hawks and Belding's ground squirrels varies from year to year apparently in accordance with January and early February weather.

The period of greatest Belding's ground squirrel abundance and vulnerability to avian predators is during the emergence and dispersal of the numerous and inexperienced young. With a cold, dry spring and a delayed reproductive cycle, the period of high abundance and vulnerability occurs in May. May is the beginning of the period of the greatest food need in Red-tailed Hawks in any year. Young hatch about the first of May, and between the third week and fledging energetic demands upon the parents are greatest (Olendorff 1974). In this case the peaks of Belding's ground squirrel abundance and vulnerability coincides closely with the needs of the Red-tailed Hawk. These are also years with high percent pair success and as a result high annual productivity.

In a year where the 174 degree date is early and above normal precipitation has occurred, the ground squirrel season is expected to

Figure 1. Red-tailed Hawk and Belding's ground squirrel reproductive chronologies. Data for Belding's ground squirrel obtained from Turner (1972).



be advanced. In this case the period of peak prey abundance and vulnerability would occur in April, well prior to the increasing food demand of Red-tailed Hawk young (mid-May). By the time Red-tailed Hawk prey needs increase, the dispersal of young Belding's ground squirrels is already well underway. These young are now somewhat experienced and most have their own burrow (Turner 1972). As such they are no longer as susceptible to predation (Craighead and Craighead 1956). These are also years when Red-tailed Hawk pair success is below average.

The degree to which peak needs in the Red-tailed Hawk and peak availability in the Belding's ground squirrel coincide appear to largely determine pair success. This has less to do with actual prey abundance than relative prey abundance. In fact, if emergence time is delayed significantly (normally benefitting Red-tailed Hawks in terms of productivity), higher mortality has been found to occur in Belding's ground squirrels (Morton and Sherman 1978). This is caused by starvation through the depletion of stored fat reserves in the Belding's ground squirrels. If actual prey abundance was the principal factor determining Red-tailed Hawk productivity, then one might expect the slope of the correlation to be reversed. Another point suggesting the lack of importance of actual prey abundance stems from the lack of correlation between Red-tailed Hawk productivity and weather of the previous growing season. Costain (1977) suggested that Belding's ground squirrel productivity is related to spring weather. These results may shed some light on the studies of McInvaille and Keith (1974) and USDI (1979) where Red-tailed Hawk productivity did not correlate well with ground squirrel numbers though they constituted a major source of prey.

The year of 1979 was a year where a marked reduction in actual prey abundance probably had a significant impact upon Red-tailed Hawk productivity. Part of the reduction in Belding's ground squirrel numbers may be attributed to an extremely cold January and, therefore, delayed onset of rapid vegetative growth and higher ground squirrel mortality. In addition, when the warm-up began in February, it occurred suddenly, and the accumulated snow melted rapidly. There was extensive flooding of many of the Belding's ground squirrel colonies undoubtedly causing greater than normal mortality (Turner 1972). Both these events worked to create an unusual prey situation. In this case, the importance of actual prey abundance apparently had a much greater impact upon Red-tailed Hawk productivity than normal.

The same kind of effect that has been observed in Belding's ground squirrels regarding timing of emergence most likely holds for the Townsend's ground squirrel as well. The impact of this apparent situation is pronounced because ground squirrels bear a single litter annually which is synchronized by the timing of emergence. This is different from most other Red-tailed Hawk prey species, notable lagomorphs and microtines (Smith and Murphy 1973; Craighead and Craighead 1956).

The effects of the timing of the onset of rapid vegetative growth may also affect other prey than ground squirrels. Pocket gophers are an important secondary prey source for Red-tailed Hawks in the Antelope area. They, as the ground squirrels, bear a single litter a year though less synchronized (Turner et al., 1973). Spring warm-up is likely to affect pocket gophers by improving foraging conditions especially in the Antelope area where snow cover is rare, and the ground is more susceptible to sub-freezing weather.

In other prey, multi-littered prey species such as lagomorphs and microtines may breed earlier in response to an advanced spring. By breeding earlier they may produce more litters and therefore more offspring. This potential increase would work counter to the pattern described above where delayed green-up benefits Red-tailed Hawk productivity. Lagomorphs and microtines are a comparatively minor prey source in this population.

Habitat also affects Red-tailed Hawk productivity. The combination of ground squirrel density and a minimum number of perches adequately dispersed throughout a territory appears to significantly affect a pair's reproductive success. Though Red-tailed Hawks hunt while in flight particularly while soaring, perches are apparently more important for hunting. It was observed here and by Fitch et al. (1946) that adequate numbers of hunting perches are apparently "the most essential feature of a territory". This is also suggested by the lack of correlation between topography and a pair's reproductive performance. The presence of hills favors both declivity winds and thermals (Cone 1962).

Perch density alone was found to be inadequate in predicting productivity. Several factors appear responsible. First, two territories with the same perch density could be quite different in suitability for hunting. A territory where the perches are poorly dispersed may leave large areas unavailable for perch hunting. Also more perches may be useful only up to a point even if they are highly dispersed. Too many perches in an area may impair hunting. Finally, ground squirrels are not normally associated with areas of high juniper density. Junipers provide the vast majority of perches. Therefore, the dispersion of perches also needs to be considered.

The perch density that appears to be required assuming adequate dispersion seems surprisingly low. This was measured at one perch per sixteenth section, but this might be an over-estimate as lesser densities above zero were not measured. Unless the Red-tailed Hawk has an effective hunting radius of 227m from these perches which average under 10m tall, they are not hunting the entire territory from these perches. Using the replacement rate of 1.35 young per pair per year (Henny and Wight 1970) for the Red-tailed Hawk and regression results here, roughly 83% of a territory needs adequate perches for a pair to be sustaining. The minimum percentage of a territory with adequate perches was 45%.

Other measures that failed to be of importance to habitat quality include surface water, wheat, and shrub density. Wheat in particular was expected to be negatively correlated with Red-tailed Hawk productivity. Annual plowing effectively eliminates prey including the Belding's ground squirrel (Turner 1972). However, the deep-soiled areas preferred for the cultivation of wheat are also preferred by the Belding's ground squirrels. Though Belding's ground squirrels cannot exist on the plowed fields, they do exist in some abundance in the remaining deep soil around the margins of the plowed fields. Shrub density was also expected to yield a negative correlation to productivity. Cave (1968) and Southern (1970) have found that raptors prefer more open areas and that it does affect hunting. The explanation here does not appear to be so clear. Junipers, however, are positively correlated with shrub density ($r = .50$).

The presence of people living on a Red-tailed Hawk territory apparently disturbs the Red-tailed Hawks little. In fact, those territories with human habitations produced significantly more young. This is attributed to several factors. First, perches in the form of utility poles and poplars and certain other trees are associated with habitations. Second, houses are generally placed near water on level ground which is also the preferred habitat of the Belding's ground squirrel (Turner 1972). Olendorff and Stoddart (1974) found that raptors nesting in remote areas and on posted land produced significantly more young. This effect is presumably due to the lack of direct human disturbance, but this effect was not considered here.

Neither territory size nor interspecific competition was correlated with territory productivity. The size of a territory says little of its quality in a heterogeneous habitat. As a general observation, territories are larger for those pairs that either have to commute some distance from the nest to an important foraging area or those pairs that have a general lack of a concentrated prey source. Because of the traditional nature of territories, boundaries were observed to change only subtly over the years. Only one significant boundary change was observed in the 31 pairs during the course of the study. Competition in this population apparently takes the form of gaining entry into one of the territories by successfully filling an opening when it appears and not in changing territory size. Though population density can have an effect upon territory size, no significant population fluctuations were observed during the study. Density was found to affect productivity in the Kestrel (Cave 1968) and in the Tawny Owl (Southern 1970). In competition with the Swainson's Hawk, the Red-tailed Hawk apparently is affected little. Those pairs regularly contesting territory each year with Swainson's Hawks fledge the same number of young as those that did not.

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