

HAWK OCCUPANCY OF DISTURBED GRASSLANDS IN RELATION TO MODELS OF HABITAT SELECTION¹

JOSEF K. SCHMUTZ

Department of Biology, University of Saskatchewan, Saskatoon, SK S7N 0W0, Canada

Abstract. I counted nesting pairs of Ferruginous Hawks (*Buteo regalis*) and Swainson's Hawks (*B. swainsoni*) on 76 41-km² study plots in 1982 and 1987 to study the effect of agricultural cultivation of grassland on hawk densities. The study plots were selected at random within a 74,686-km² mixed-grass prairie region in southeastern Alberta. The results confirm a curvilinear relationship between hawk density and extent of cultivation. Nesting densities of both species were higher in areas of moderate cultivation than in grassland. On plots with extensive cultivation (>30%), Ferruginous Hawks declined and so did ground squirrels, their main prey. Swainson's Hawks did not decline with extensive cultivation but probably shifted to other prey where ground squirrels were scarce. The observed curvilinear relationship between hawk density and habitat is similar in shape to changes in the productivity of ecosystems subjected to varying degrees of disturbance.

The pattern of hawk abundance in relation to habitat quality did not change between years despite a more than 50% increase in hawk densities. The hawks therefore did not conform to the general assumption in models of habitat selection that optimal habitats are saturated before suboptimal areas are occupied. Instead, new breeding pairs continued to settle in optimal habitat but not suboptimal habitat. To account for these results, I propose a graphical model which incorporates territoriality as a factor causing regular dispersion at medium population densities across the range of habitat types included in this study. Optimal habitat may be the last to reach saturation because only there can territory size be reduced furthest under increasing intruder pressure.

Key words: *Ferruginous Hawk; Buteo regalis; Swainson's Hawk; Buteo swainsoni; Alberta; habitat-selection models; grassland cultivation; population dynamics; territoriality.*

INTRODUCTION

The large number of published reports that describe habitat selection among birds attests to the enormous variation observed and to the biological importance of this topic. In addition to its basic biological importance, an understanding of the responses by birds, and other animals, to changes in habitat characteristics is important for conservation. Habitat degradation emerges as a major threat to conservation in many countries.

Functional and theoretical aspects of habitat selection have been summarized by Cody (1985). Fretwell and Lucas (1970) and Fretwell (1972) provide a theoretical framework for habitat selection. Their model illustrates the choices individuals are forced to make when attempting to maximize fitness in habitats varying in suitability for optimal survival and reproduction. They postulate first that organisms are able to judge an area's basic suitability and seek those areas best suited ("ideal distribution"). Second, under increasing intruder pressure suitability decreases

and individuals disperse ("free distribution"), such that in the end they experience relatively equal feeding opportunity in sites varying in resource availability. Given differences in suitability between habitats, the prediction is that areas of lower suitability are occupied only after the suitability of the most optimal areas has been reduced by the need to share resources with others. The model predicts that members of a species for which this model applies experience relatively equal habitat suitability and hence equal fitness for that component of fitness that is derived from habitat suitability.

Species that exhibit territoriality such that their density can be greatly dependent on this behavior (e.g., Brown 1969), violate the "free" assumption of the ideal free distribution model. To include the effect of dominance and territoriality, Fretwell (1972) incorporated a risk accruing to unsettled individuals in the "ideal despotic distribution model." Because territories are generally smaller and hence more easily defended in the most suitable areas, territoriality can create differences in fitness between individuals in areas differing in their basic suitability.

¹ Received 27 September 1988. Final acceptance 30 January 1989.

In this analysis, I report on a "natural experiment" in which the habitat selection of Ferruginous and Swainson's hawks was studied twice, 5 years apart, on randomly selected study plots in southeastern Alberta. During the 5-year interim, the abundance of Richardson's ground squirrels (*Spermophilus richardsonii*) has increased markedly (J. K. Schmutz and D. J. Hungle, unpubl. data), and so has the population density of both hawks (Schmutz, unpubl.). The study plots used were the same in both years. Changes in the degree of cultivation between years were small. In a within-year comparison, I examine differences in the densities of breeding hawks between plots varying in degree of cultivation. I also examine habitat selection between years when the overall population size of hawks differed. The observed patterns of habitat selection are compared with predictions based on models of habitat selection. I make the fundamental assumption in this analysis that individuals on different plots are drawn at random from the population pool and that they do not represent different ecotypes.

The Ferruginous and Swainson's hawks studied exhibit intraspecific territoriality (Schmutz et al. 1980, unpubl.). Their habitat selection has been described (Olendorff 1973; Schmutz et al. 1980; Bechard 1982; Gilmer and Stewart 1983, 1984; Schmutz 1984, 1987; Janes 1985). Unlike Swainson's Hawks, Ferruginous Hawks are highly selective in their choice of grassland habitat for nesting. This habitat dependence is so pronounced that an availability of grassland has been considered important in limiting this species' breeding distribution.

The present study differs from most others (cf. Cody 1985) in some potentially important ways. First, the species studied are large raptors which, as adults at least, are threatened by few if any heterospecific predators. Second, density is that of breeders only. Third, comparisons of hawk density are made within a grassland habitat that varies in degree of disturbance due to agricultural cultivation. Thus, this study examines responses by the hawks to alterations (cultivation) of one type of habitat (mixed-grass prairie) and not differences between two natural habitats.

STUDY AREA AND METHODS

Nesting pairs of Ferruginous and Swainson's hawks were counted on 41-km² study plots se-

lected at random within a 74,686-km² survey region in southeastern Alberta. This region was bounded by Saskatchewan and Montana. Within Alberta, the study area included semi-arid, mixed-grass prairie habitat located south of 51°42'N latitude and east of 114°00'W longitude. I searched plots for nests in 2 years. In 1982, I searched 80 plots (Schmutz 1984) and in 1987, 78 plots, 76 of which were searched during both years.

I searched study plots completely for all nests of buteonine hawks. The primary mode of transportation on plots was by motorcycle but some sites were searched using a truck or on foot. In most areas, nests were found easily in the gently undulating landscape with few trees. In addition to nests containing eggs or young, some deserted nests (4.7% of all nests) that showed evidence of use during the present year (Postupalsky 1974) were counted. In these cases, species was determined by the type of nest material (Schmutz et al. 1980) and color of feathers present. The 6-week searching period, from late May to early July, included the hatching and nestling periods of Ferruginous Hawks, and the latter part of laying, all of incubation, and the early nestling period of Swainson's Hawks.

Steeply eroded banks existed on the study area along rivers and creeks. Some grasslands had never been tilled, others had undergone secondary succession from fields abandoned during the 1930s (Dormaar and Smoliak 1985). The primary land uses were grazing of cattle and growing of cereal grain, depending on soil quality for agriculture and nature of terrain. In 1982 the average percent cultivation was 50% and in 1987 it was 53%.

For each plot, the locations of nests, fields, pastures, trees, and water bodies were recorded on a data sheet at the time of searching. I determined the percentage of land area that was cultivated from these maps for each year separately. Fields that had been reseeded with "tame" grass varieties and used for grazing were recorded as grassland. Fields of clover, that were irrigated and used for forage production, were recorded as cultivated because of their similarity to cereal crops in vegetation height and density.

I recorded the number and activity of hawks present when their nest was found. Nest contents were inspected when accessible without climbing aids. In late May and early June, clutches of Swainson's Hawks were considered complete if

down feathers were present in the nest cup and the incubating hawk flushed at a distance of 20 m or less. Because the nests were visited only once between the latter period of laying (Swainson's) and pre fledging (Ferruginous), the number of eggs or young, found on different days from the mean hatching date, was expressed as a deviation from a local population average. This allowed a comparison between pairs on different plots. An average clutch and a change in brood size throughout the nestling period was derived from a total of 29 nests of Ferruginous Hawks and 25 nests of Swainson's Hawks monitored on the Hanna study area in 2 years (Schmutz et al. 1980). Those nests were visited for a study of food habits every 1–3 days beginning prior to hatching. Most loss of nestlings occurred early with little change in the second half of the nestling period (J. K. Schmutz, unpubl. data). I consider the Hanna study area representative of many plots because this area was located in the north-central portion of the survey region (Schmutz, unpubl.) and because 14% of the area was cultivated.

To monitor the abundance of the hawks' main prey, I recorded the number of burrows showing signs of use by ground squirrels (*Spermophilus* spp.) on transects within study plots in 1987. One to four transects were done on each of 37 plots which contained at least 3 km² of contiguous grassland. Burrows within 1 m of an observer were counted while driving a motorcycle at slow speed in a straight line. Transect length varied from 0.5 to 1.5 km depending on accessibility.

Assumptions of normality were not met in the data. Hence, tests of significance were fraught with difficulty when using parametric statistical approaches for hypothesis testing. Nonparametric approaches were also not entirely valid in all cases owing to up to 27% tied values. I therefore used a combination of nonparametric, and parametric analyses (Feldman et al. 1986). The null hypothesis was rejected at the 0.05 level.

RESULTS

Hawk density and distribution on study plots was potentially affected by nest-site availability, degree of cultivation, inter- and intraspecific competition, and hawk population size. While degree of cultivation was the primary factor examined in this study, other factors may have interacted with it. An influence of nest-site availability on hawk density has been shown previ-

ously (Schmutz et al. 1980, 1984). To minimize the confounding influence of tree availability on hawk density, I excluded plots which bore no trees. This approach was slightly conservative because some pairs could nest on the ground. Fifteen percent of Ferruginous Hawks and <1% of Swainson's Hawks nested on the ground. In an attempt to account for intraspecific territoriality, some treed plots were also excluded if every 0.64 km² (quarter section) of treed land supported a conspecific, nesting pair of hawks. The number of plots that remained for analysis was 66 for Ferruginous Hawks and 64 for Swainson's Hawks.

CULTIVATION AND HAWK DENSITY

Cultivation on plots ranged from 0 to 99%, excepting farmyards and roadsides. In a curvilinear relationship, the hawks increased in density where cultivation increased up to 30% and then either declined (Ferruginous Fig. 1) or showed no further change (Swainson's Fig. 2).

To determine whether the observed curvilinear relationship between hawk density and cultivation differed significantly from a straight line, I first compared hawk density on plots of grassland (0–10% cultivation) with plots of moderate cultivation (11–30%) in an a posteriori manner. For each species and during each year, the mean number of nests was greater in areas with 11–30% cultivation than 0–10% (Table 1). When the apparently positive effect of moderate cultivation on hawk density was excluded by considering only plots with 11–100% cultivation, Ferruginous Hawks declined with increasing cultivation (1982: Spearman's $r_s = -0.477$, $P = 0.003$; 1987: $r_s = -0.684$, $P < 0.001$). Swainson's Hawks, in contrast, showed no significant declining trend with increasing cultivation (1982: $r_s = -0.149$, $P = 0.134$; 1987: $r_s = -0.042$, $P = 0.377$).

The number of suitable nest trees on a plot was dependent on land use. Frequently, trees were planted as "shelterbelts" near fields, trees were protected from damage by livestock when growing near fields, and trees benefitted from additional moisture present in the irrigated/cultivated regions. In an additional attempt to separate the effect of tree availability (number of 0.64 km² per plot bearing one or more trees/shrubs) from the effects of cultivation on hawk density, I used a multiple regression analysis after hawk density was subjected to square root transformation. This

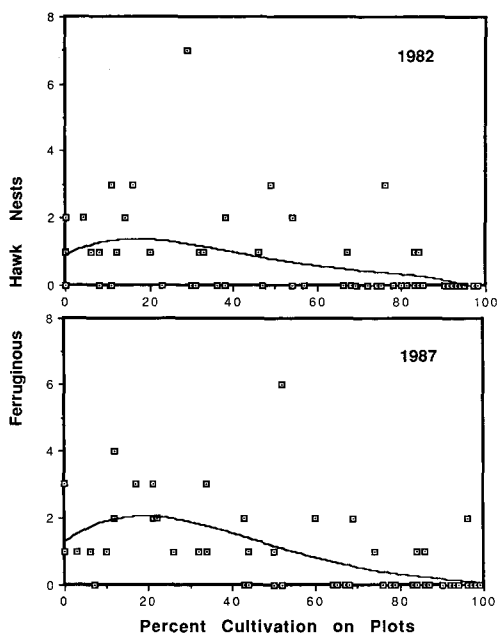


FIGURE 1. The number of nests of Ferruginous Hawks on plots in 1982 and 1987 are shown in relation to the percent cultivation on plots. A fourth order polynomial expression, represented by a line, was fitted to the data by increasing the order of the expression until no further resolution in the shape of the curve was obtained. The mean number of nests in each 10% cultivation category and the range in the number of nests are given in Table 2.

was done to ensure that the hawks' responses to habitat change (cultivation) did not merely reflect tree availability. For this analysis I used all 76 plots searched in 1982 and 1987. In the case of Ferruginous Hawk density, there was no improvement in the amount of variation explained when the additional variable of tree availability was added to cultivation (1982: cultivation $r^2 = 0.210$, cultivation and trees $r^2 = 0.190$; 1987: cultivation $r^2 = 0.417$, cultivation and trees $r^2 = 0.344$). By nesting on the ground, on rocks or on man-made structures (Schmutz et al. 1984), Ferruginous Hawks were able to occupy areas where trees were absent. Swainson's Hawk density was more strongly affected by tree availability. The square of the regression coefficient for cultivation was substantially greater when trees were added as a variable (1982: cultivation $r^2 = 0.070$, cultivation and trees $r^2 = 0.288$; 1987: cultivation $r^2 = 0.148$, cultivation and trees $r^2 = 0.255$).

To examine a possible link between hawk density and cultivation, I plotted ground squirrel

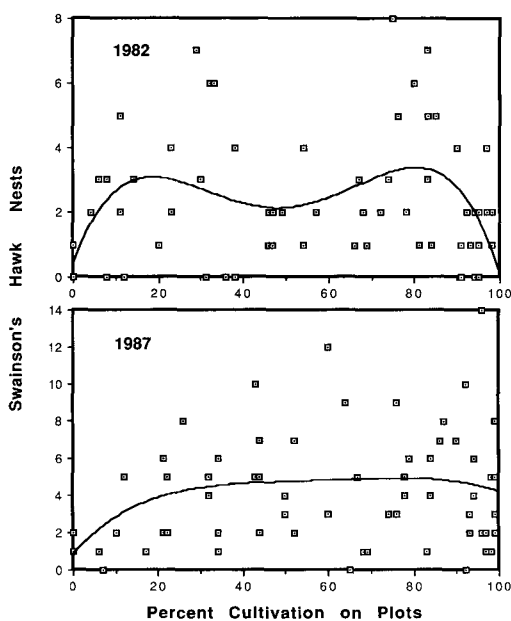


FIGURE 2. The number of nests of Swainson's Hawks on plots in 1982 and 1987 are shown in relation to percent cultivation on plots. A fourth order polynomial expression was fitted to the data (see Fig. 1). The mean number of nests in each 10% cultivation category and the range in the number of nests are given in Table 2.

abundance with percent cultivation on plots. Squirrel abundance was most variable on plots with little or no cultivation (Fig. 3). Because of their loosely colonial dispersion, squirrels were sometimes abundant on small patches of grassland. The decline in squirrel abundance on a plot basis was actually much greater than suggested by these data because squirrels occupied cropland at low density if at all and no burrow counts were carried out there. Squirrel abundance relative to cultivation resembled the Ferruginous Hawks' density pattern. Squirrels appeared to increase in abundance with an increase in cultivation up to 30% (Fig. 3). However, this increase was not statistically significant ($r_s = 0.256$, $n = 27$, $P = 0.096$), possibly because of a wide variance in burrows counted and a small sample of transects. Squirrels declined where the degree of cultivation exceeded 30% ($r_s = -0.649$, $n = 26$, $P < 0.001$).

HAWK REPRODUCTION IN RELATION TO HABITAT

In 1987, even those pairs that nested on the most intensively cultivated plots raised a normal number of young. Four pairs of Ferruginous Hawks,

TABLE 1. The number of nesting pairs of Ferruginous and Swainson's hawks on plots in grassland (0–10% cultivation) and on plots with moderate cultivation (11–30%) in southeastern Alberta. Differences in nesting density between the two cultivation categories are compared using a modified sign test (Conover 1971). I recorded the number of plots whose densities were above or below the combined mean density (\bar{x}) for all 35 or 31 plots combined. This method assumes that if hawk density were not affected by the degree of cultivation, a similar proportion of plots in each cultivation category would fall above or below the combined mean.

	Grassland				Moderate cultivation			
	\bar{x}	Range	<i>n</i>	Plots above \bar{x}	\bar{x}	Range	<i>n</i>	Plots above \bar{x}
Ferruginous								
1982	0.88	0–2	8	2 (25%)	1.54	0–7	11	4 (36%)
1987	1.14	0–3	7	1 (14%)	2.44	0–4	9	8 (89%)
Total	1.00	0–3	15	3 (20%)	1.95	0–7	20	12 (60%) ^a
Swainson's								
1982	1.43	0–3	7	2 (29%)	3.00	0–7	10	6 (60%)
1987	1.33	0–2	6	0	4.38	0–8	8	5 (63%)
Total	1.38	0–3	13	2 (15%)	3.61	0–8	18	11 (61%) ^b

^a $\chi^2 = 5.60, P = 0.018$.

^b $\chi^2 = 6.48, P = 0.011$.

for which the brood size was known and which nested on plots with 70% or more cultivation, raised 2.8 young, compared to 3.0 young raised by 59 pairs on the Hanna study area in 1987. Similarly, 10 pairs of Swainson's Hawks on plots with 90% or more cultivation raised 2.3 young, the same number that was raised by 81 pairs on the Hanna study area. Furthermore, using the coarse measure of reproduction obtained in this study, there was no evidence to suggest that reproductive performance declined as degree of cultivation increased (Ferruginous $r_s = -0.070$, $n = 30$, $P = 0.353$; Swainson's $r_s = 0.086$, $n = 77$, $P = 0.228$).

POPULATION SIZE AND HABITAT OCCUPANCY BETWEEN YEARS

Populations of nesting Ferruginous and Swainson's hawks have increased by 60% and 57% respectively between 1982 and 1987 following a regional increase in the abundance of ground squirrel prey (J. K. Schmutz and D. J. Hungle, unpubl. data). The additional hawks that nested in 1987 could have settled in one of three ways: (1) in each cultivation category in equal numbers, (2) in the same proportions as they nested in 1982, or (3) preferentially in areas with either a low or high degree of cultivation.

An increase in density of Ferruginous Hawks between 1982 and 1987 occurred primarily in the 11–40% cultivation categories (Table 2), preferentially near the low end of the cultivation continuum. The increase in nests in the 0–10% category was small. Areas of extensive cultivation

were avoided. The pattern of occupancy was highly similar between years.

The additional Swainson's Hawks that nested in 1987 also exhibited a habitat preference. In contrast to Ferruginous Hawks, this preference was for moderately and extensively cultivated areas. Only plots with 0–10% cultivation were avoided (Fig. 1). Again, the pattern of occupancy was similar between years.

COMPETITION

Although most new pairs of Ferruginous Hawks in 1987 colonized plots in the 11–40% cultivation range, their settlement on individual plots depended on previous densities. Ferruginous Hawk numbers tended not to change or to decrease on those plots on which pairs already nest-

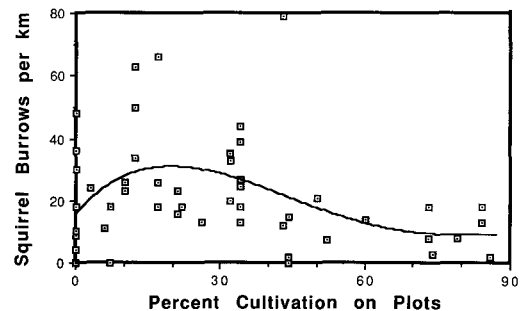


FIGURE 3. The number of ground squirrel burrows counted on transects on the grassland portion of study plots in relation to the degree of cultivation on plots. A fourth order polynomial expression was fitted to the data (see Fig. 1).

TABLE 2. The mean number of Ferruginous and Swainson's hawk nests in each cultivation category in southeastern Alberta is shown including sample range and the number of plots in each category. Only those plots which bore unused nest trees are included here.

	Percent cultivation on plots										Total
	0-10	11-20	21-30	31-40	41-50	51-60	61-70	71-80	81-90	91-100	
Ferruginous Hawk											
1982											
Mean	0.88	1.67	1.40	0.67	1.00	0.67	0.25	0.43	0.25	0.00	0.62
Range	0-2	0-3	0-7	0-2	0-3	0-2	0-1	0-3	0-1	0	0-7
Plots	8	6	5	6	5	3	4	7	8	14	66
1987											
Mean	1.14	3.00	2.17	1.80	0.86	2.50	0.40	0.17	0.29	0.13	0.94
Range	0-3	2-4	1-3	1-3	0-3	0-6	0-2	0-1	0-1	0-2	0-6
Plots	7	3	6	5	7	4	5	6	7	16	66
Mean increment	0.26	1.33	0.77	1.33	-0.14	1.83 ^a	0.15	-0.26	0.04	0.13	
Swainson's Hawk											
1982											
Mean	1.43	2.20	3.80	2.67	1.60	2.33	1.75	4.57	3.38	1.36	2.44
Range	0-3	0-5	2-7	0-6	1-2	1-4	1-3	2-8	1-7	0-4	0-8
Plots	7	5	5	6	5	3	4	7	8	14	64
1987											
Mean	1.33	3.00	4.83	3.60	4.86	6.00	3.20	5.00	5.71	4.13	4.23
Range	0-2	1-5	2-8	1-6	2-10	2-12	0-9	3-9	1-8	0-14	0-14
Plots	6	2	6	5	7	4	5	6	7	16	64
Mean increment	-0.10	0.80	1.03	0.93	3.26	3.67	1.45	0.43	2.33	2.77	

^a This increase was due to one plot with 7 nests and 29% cultivation in 1982 and 6 nests and 52% cultivation in 1987.

ed in 1982. Conversely, on plots where no hawks were found in 1982 nesting densities tended to increase (Table 3). Swainson's Hawks showed no evidence to suggest that 1982 density affected settlement in 1987 (Table 3).

TABLE 3. The number of plots on which density changed in 1987 as compared to 1982 in relation to the nesting density in 1982. Rows and columns are collapsed so that the sample size in each cell is maximized (Conover 1971).

Change in 1987	Number of nests in 1982		
	0	1-7	
Ferruginous Hawk^a			
Increase	13	8	
No change	31	4	
Decrease	0	10	
Change in 1987	Number of nests in 1982		
	0-1	2-3	4-8
Swainson's Hawk^b			
Increase	20	17	10
Decrease/no change	5	6	5

^a $\chi^2 = 28.06, P < 0.001.$

^b $\chi^2 = 3.56, P = 0.470.$

It is conceivable that one species of hawk gained a competitive advantage in some habitat types and displaced the other accordingly. This was unlikely because no significant negative relationship between the densities of the two species within years could be found on the 76 plots (1982: $r_s = 0.230, P = 0.025$; 1987: $r_s = -0.005, P = 0.484$). Furthermore, in 1987, the year with greatest densities, correlations between densities of the two species had a positive sign whether cultivation ranged from 0-50% or 51-100%.

DISCUSSION

HABITAT AND HAWK DENSITY

The results confirm that cultivation was important in determining Ferruginous and Swainson's hawk distribution. Hawk response to habitat change was curvilinear. Despite a negative effect on density when cultivation was extensive (>30%), Ferruginous Hawks occupied areas of moderate cultivation (10-30%) at greater density than they did grassland. Ferruginous Hawks were habitat specialists (e.g., Rosenzweig 1981). Their density reached a distinct peak along the habitat

continuum. Swainson's Hawks were largely opportunistic because their densities changed little on plots with 11–100% cultivation. Although Ferruginous and Swainson's hawks used similar resources on the Hanna study area (Schmutz et al. 1980), they responded differently to habitat alteration. Swainson's Hawks preferred cultivated areas over grassland regardless of the extent of cultivation.

The shape of the curvilinear response to cultivation, particularly by Ferruginous Hawks, resembled a well-documented general pattern exhibited by ecosystems responding to disturbance. Reimer (1983) found that as the frequency of disturbance increased, net primary productivity in grassland or forest ecosystems also increased, but only at low disturbance levels. Net primary productivity declined as disturbance increased further. During this study disturbance (cultivation) was similar between plots in the number of times with which it occurred but the aerial extent of this disturbance on a plot varied. The outcome of cultivation was a checkered distribution of grassland and fields with varying degrees of habitat edge. A lack of a decline in Swainson's Hawk density with increasing cultivation was consistent with this species' generalized food habits. Where ground squirrels became scarce, Swainson's Hawks probably fed on cricetid rodents and grasshoppers.

The results confirm Rosenzweig's (1981) assumption that habitat selection is independent of bird density. Despite a more than 50% increase in breeding density, the pattern of hawk abundance remained the same. This result was surprising because it may be expected that intra- and interspecific competition under increased nesting densities may alter the hawk distribution pattern along the habitat continuum. The specializations in resource utilization within a species on the one hand and the limitations faced by individuals on the other (e.g., adaptations to cope with aridity), may be far more important in determining habitat distribution than the actions of competitors.

HABITAT AND FOOD

Changes in prey densities on plots between years were not recorded during this study. However, data on the amount of poison used by landowners in the northern 12% of the survey region suggest that ground squirrels have increased in abundance in 1986 (J. K. Schmutz and D. J.

Hungle, unpubl. data). The similarity between Ferruginous Hawk and ground squirrel abundance in relation to cultivation on plots supports the view that food availability is a prominent factor determining bird density and distribution (e.g., Newton 1980). Ferruginous Hawks relied primarily on ground squirrels for food (Schmutz et al. 1980) and hence it is not surprising that this hawk's pattern of abundance is similar to the abundance of ground squirrels. This hawk's response to habitat modification may have been mediated by the response of ground squirrels. Swainson's Hawks, in contrast, raised more young when they nested near fields on the Hanna study area (Schmutz 1987).

In this study, hawk density was more strongly influenced by cultivation than was hawk reproduction. This may indicate that the hawks accurately assessed the suitability of a given nesting area before they attempted to breed there. This would therefore support Fretwell's (1972) notion of an "ideal distribution."

COMPETITION

The avoidance by newly settling Ferruginous Hawks of plots that, although basically suitable, were already occupied by conspecifics agrees with results from the Hanna study area. Evidence there suggested that a surplus of breeders, especially among Ferruginous Hawks, was prevented from breeding by the territorial competition for space by nearby residents (Schmutz, unpubl.). In view of the extensive loss of grassland in western Canada and given this species' dependence on grassland, the existence of a surplus of breeders is not surprising. The Canadian breeding range of Ferruginous Hawks is smaller now than it was in the past (Schmutz 1984). Swainson's Hawks used smaller territories and may not yet have reached densities at which territoriality limited their nesting density. This may be so even though the densities encountered in this study were among the highest reported for these species.

Despite exceptionally high densities of both species of hawks on many plots, there was no evidence for one species displacing another from plots. The two species maintained intraspecific but not interspecific territories on the Hanna study area (Schmutz et al. 1980). When a shortage of nests forced the later arriving Swainson's Hawk to nest near Ferruginous Hawks, aggression between pairs has resulted in reduced reproductive success. Interspecific aggression may have oc-

curred in this study also, but interspecific competition apparently played a minor role if any in affecting densities.

MODELS OF HABITAT SELECTION

The preferential settlement of optimal habitat by new hawks in 1987 was contrary to predictions arising from models of habitat selection. Newly settling hawks did not "spill over" into suboptimal plots within their breeding range as expected (Fretwell and Lucas 1970, Fretwell 1972, Klomp 1972, Grant 1975). The expectation that birds settle optimal habitat first and spill over into suboptimal space later is rooted in optimal foraging and competition theory (Rosenzweig 1985) and has considerable empirical support from other studies (Cody 1985).

Before the applicability of models of habitat selection is evaluated in the context of this study, it may be instructive to examine first whether special conditions (e.g., philopatry) violated fundamental assumptions of the model and not the model itself. Philopatric tendencies among animals may affect habitat selection by restricting the freedom to disperse (Fretwell 1972, Cody 1985). Such restrictions to dispersal among breeders may be related to selection manifested in local adaptation (e.g., Mayr 1963) or optimal inbreeding (e.g., Shields 1982). Fretwell (1972) suggests that in such cases habitat selection should be considered only among members of local populations. Given the checkered distribution of plots with varying degrees of cultivation and the comparatively high natal dispersal exhibited by the hawks (J. K. Schmutz, unpubl. data), philopatry is unlikely to be a complicating factor in this study.

Wiens et al. (1986) concluded that philopatry was responsible for a time lag in the response by breeding birds to experimental manipulations of habitat quality. Given the long history of cultivation in the study region and the 5 years between counts, any time lag in response probably would have been of minor importance. Furthermore, it is presumably the newly settling individuals that behaved contrary to expectation and not established breeders.

The data suggest a new model for the occupancy of habitat by the species studied (Fig. 4). This model may only apply to species in which individuals defend all-purpose territories and in which territoriality can limit density (Brown 1969, Fretwell 1972). The model presupposes

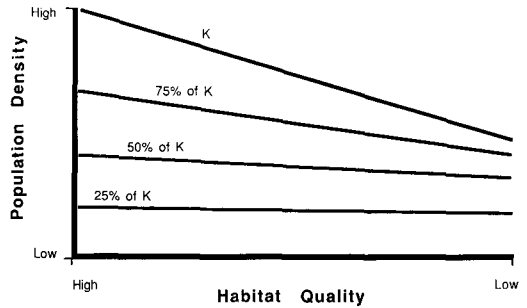


FIGURE 4. Presumed pattern by which habitat varying in quality is occupied by the hawks (see text). The area under each line represents 25% of the total carrying capacity K . The negative slope of the lines increases as population density approaches K .

that all potential settlers are equally well adapted to exploit the habitat in question and are thus equally free to enter those habitats.

In the context of the hawks studied, the model may be interpreted as follows. At low densities in the past (e.g., 25% of carrying capacity), the hawks may have occupied habitats of different quality at relatively equal density. Any negative slope in density across a habitat continuum may have been statistically indistinguishable from zero slope (Fig. 4). In the absence of the stabilizing effect of territoriality, dispersion may have been close to random and density in a given area variable over time. Only as density increased (e.g., up to 75% of carrying capacity) may a habitat preference have become evident, as it did in the 1982 data. When hawk density approached carrying capacity in 1987, the less suitable habitat could apparently no longer accommodate additional pairs. On the Hanna study area at least, breeding pairs deviated from a random toward a regular pattern of dispersion (Schmutz et al. 1980). The rapid replacement of six dead adults on the Hanna study area in recent years suggested that a surplus of potential breeders existed and that most or all available breeding opportunities were saturated (Schmutz, unpubl.). The proposed model is consistent with Fretwell's (1972) despotic distribution in that those individuals occupying the most suitable areas may be able to defend concentrated resources with comparatively less expenditure of energy and time, and may survive and reproduce more successfully than individuals occupying less suitable areas.

One possible functional explanation for the described pattern (Fig. 4) includes a tendency for

individuals to claim more space in optimal areas under low intruder pressure than is required to obtain resources necessary for successful reproduction. This is not to imply a "superterritory" (see Verner 1977, Colgan 1979, Robertson and Gibbs 1982). The defense of a larger than required territory is contrary to a substantial body of evidence that suggests that many birds minimize territory size and maximize benefit (Davies 1980). However, most studies addressing this question are carried out in high density areas where territorial optimization may be expected. An avoidance of distant neighbors at low density may be subtle (Tinbergen 1967) and serve to reduce interference during pair formation and mating (Hinde 1965, Wells 1977).

Reasons for the unexpected settlement in the optimal and not the suboptimal areas may include unequal changes in suitability. For example, a given patch may be suitable for occupancy by an individual if conditions along each of 10 different resource gradients reached or exceeded a threshold level. Patches in optimal habitat may on average contain more resource dimensions above threshold than patches in suboptimal habitat. Even if a beneficial change occurs across all habitats and even if this change (e.g., climatic changes) causes improvements in two or more resource dimensions, there will be a greater likelihood that patches in the optimal as opposed to suboptimal habitat will become suitable for occupancy. This could explain why new individuals could settle in the already densely occupied areas and not in the sparsely occupied suboptimal habitat.

ACKNOWLEDGMENTS

I gratefully acknowledge the field assistance provided by R. G. Johnson, R.J.P. Meschishnick, and H. P. Samoil. S. M. Schmutz contributed to many aspects of this study. K. Martin, F. Messier, and anonymous referees provided helpful discussion and comments on this manuscript. M. G. Bickis kindly provided statistical advice. Financial support was provided by the Alberta Recreation, Parks and Wildlife Foundation, the World Wildlife Fund Canada, the Alberta Division of Fish and Wildlife, the Canadian Wildlife Service, the Special Areas Board of Hanna, and the University of Saskatchewan.

LITERATURE CITED

- BECHARD, M. J. 1982. Effect of vegetative cover on foraging site selection by Swainson's Hawk. *Condor* 84:153-159.
- BROWN, J. L. 1969. Territorial behavior and population regulation in birds. *Wilson Bull.* 81:293-329.
- CODY, M. L. 1985. *Habitat selection in birds*. Academic Press, New York.
- COLGAN, P. 1979. Is a superterritorial strategy stable? *Am. Nat.* 114:604-605.
- CONOVER, W. J. 1971. *Practical nonparametric statistics*. John Wiley and Sons, New York.
- DAVIES, N. B. 1980. The economics of territorial behavior in birds. *Ardea* 68:63-74.
- DORMAAR, J. F., AND S. SMOLIAK. 1985. Recovery of vegetative cover and soil organic matter during revegetation of abandoned farmland in a semiarid climate. *J. Range Manage.* 38:487-491.
- FELDMAN, D. S., JR., J. GAGNON, R. HOFMAN, AND J. SIMPSON. 1986. *Stat-View 512+*. Brain Power, Calabasas, CA.
- FRETWELL, S. D. 1972. *Populations in a seasonal environment*. Princeton Univ. Press, Princeton, NJ.
- FRETWELL, S. D., AND H. L. LUCAS. 1970. On territorial behavior and other factors influencing habitat distribution in birds. *Acta Biotheor.* 19:16-36.
- GILMER, D. S., AND R. E. STEWART. 1983. Ferruginous Hawk populations and habitat use in North Dakota. *J. Wildl. Manage.* 47:146-157.
- GILMER, D. S., AND R. E. STEWART. 1984. Swainson's Hawk nesting ecology in North Dakota. *Condor* 86:12-18.
- GRANT, P. R. 1975. Population performance of *Microtus pennsylvanicus* confined to woodland habitat, and a model of habitat occupancy. *Can. J. Zool.* 53:1447-1465.
- HINDE, R. A. 1956. The biological significance of territories of birds. *Ibis* 98:340-369.
- JANES, S. W. 1985. Habitat selection in raptorial birds, p. 159-188. *In* M. L. Cody [ed.], *Habitat selection in birds*. Academic Press, New York.
- KLOMP, H. 1972. Regulation of the size of bird populations by means of territorial behavior. *Neth. J. Zool.* 22:456-488.
- MAYR, E. 1963. *Animal species and evolution*. Belknap Press, Cambridge, MA.
- NEWTON, I. 1980. The role of food in limiting bird numbers. *Ardea* 68:11-30.
- OLENDORFF, R. R. 1973. The ecology of nesting birds of prey of northeastern Colorado. U.S. Int. Biol. Program, Grassland Biome, Tech. Report 211.
- POSTUPALSKY, S. 1974. Raptor reproductive success: Some methods, criteria and terminology, p. 21-31. *In* F. N. Hamerstrom, Jr., B. E. Harrell, and R. R. Olendorff [eds.], *Management of raptors*. Raptor Research Foundation, Vermillion, SD.
- REIMER, W. A. 1983. Disturbance and basic properties of ecosystem energetics, p. 83-98. *In* H. A. Mooney and M. Godron [eds.], *Disturbance and ecosystems*. Springer-Verlag, New York.
- ROBERTSON, R. J., AND H. L. GIBBS. 1982. Superterritoriality in tree swallows: A reexamination. *Condor* 84:313-316.
- ROSENZWEIG, M. L. 1981. A theory of habitat selection. *Ecology* 62:327-335.
- ROSENZWEIG, M. L. 1985. Some theoretical aspects of habitat selection, p. 517-540. *In* M. L. Cody

- [ed.], Habitat selection in birds. Academic Press, New York.
- SCHMUTZ, J. K. 1984. Ferruginous and Swainson's hawk abundance and distribution in relation to land use in southeastern Alberta. *J. Wildl. Manage.* 48:1180-1187.
- SCHMUTZ, J. K. 1987. The effect of agriculture on Ferruginous and Swainson's hawks. *J. Range Manage.* 40:438-440.
- SCHMUTZ, J. K., S. M. SCHMUTZ, AND D. A. BOAG. 1980. Coexistence of three species of hawks (*Buteo* spp.) in the prairie-parkland ecotone. *Can. J. Zool.* 58:1075-1089.
- SCHMUTZ, J. K., R. W. FYFE, D. A. MOORE, AND A. R. SMITH. 1984. Artificial nests for Ferruginous and Swainson's hawks. *J. Wildl. Manage.* 48:1009-1013.
- SHIELDS, W. M. 1982. Philopatry, inbreeding and the evolution of sex. State Univ. of New York Press, Albany, NY.
- TINBERGEN, N. 1967. Adaptive features of the Black-headed Gull *Larus ridibundus*. *Proc. XIV Int. Ornithol. Congr.* (1966):43-59.
- VERNER, J. 1977. On the adaptive significance of territoriality. *Am. Nat.* 111:769-775.
- WELLS, K. D. 1977. Territoriality and male mating success in the green frog (*Rana clamitans*). *Ecology* 58:750-762.
- WIENS, J. A., J. T. ROTENBERRY, AND B. VAN HORNE. 1986. A lesson in the limitations of field experiments: Shrub-steppe birds and habitat alteration. *Ecology* 67:365-376.