

AN ABSTRACT OF THE THESIS OF

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Rates of predation on artificial nests and nests of pen-reared ring-necked pheasants (Phasianus colchicus), released in spring, were compared between strip and block habitats at different densities of nests. Nests in strips had rates of predation 4-7 times greater than nests in blocks, regardless of nest density. Differences between successful and depredated nests were due primarily to differences in habitat pattern rather than structural characteristics of vegetation at nest sites. Predators may be able to control prey populations in habitats where prey are concentrated and effectiveness of predators is high, therefore predation could be viewed as acting in a density-independent manner.

RELATIONSHIPS BETWEEN DEPREDATION OF NESTS OF
GROUND-DWELLING BIRDS AND HABITAT STRUCTURE AND PATTERN

by

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CONTRIBUTIONS OF AUTHORS

Creation of this document entailed development of the thesis topic, design of the study, collection and analysis of data, and writing and reviewing the manuscript. John Crawford reviewed numerous drafts of the thesis and was instrumental in developing the thesis topic and designing the study. Mark Meyers assisted in designing parts of the study and collected the data in 1980 and 1981.

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RELATIONSHIPS BETWEEN DEPREDATION OF NESTS OF GROUND-DWELLING
BIRDS AND HABITAT STRUCTURE AND PATTERN

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INTRODUCTION

Theories of density dependence and thresholds of security are central to discussions on predation. McAtee (cited in Errington 1935) stated predation was directly related to numbers of prey and rates of predation increase and decrease in proportion to increases and decreases in prey populations. Errington (1945) described the threshold of security as the population level below which prey populations are free from non-emergency (i.e. density-dependent) losses; and once numbers of prey exceed the threshold, rates of predation become dependent on density of prey. Leopold (1933:231) suggested that in addition to density of predators and prey, behavior of predators, density of alternative foods, and physical condition of prey influenced rates of predation.

Predation as a density-dependent process is viewed as having the capacity to regulate a population by removal of "surplus" individuals (Errington 1946, Holling 1959). In contrast, density-independent

processes (e.g. effects of adverse weather) could be viewed as having the capability of limiting or controlling prey populations by depressing numbers of prey below the threshold of security. No one has proposed in the literature that the action of predation could be density-dependent under one set of circumstances and density-independent under another. Gottfried (1978) alluded to this possibility after finding no difference in rates of predation on artificial nests in two vegetatively similar plots with different densities of nests. But, he concluded no generalizations could be made about relationships between density of nests and rates of predation in upland habitats.

Predation presumably could be considered density-independent if after the removal or reduction of predators, prey populations increased. Balser et al. (1968) concluded increased production by waterfowl resulted from control of predators. Schranck (1972) reported higher nest success for waterfowl on areas with control of predators. Glading et al. (1945) attributed increased numbers of California quail (Callipepla californicus) to control of predators and artificial feeding. Trautman et al. (1974) found an increase of 132% in numbers of ring-necked pheasants on an area where mammalian predators were removed.

In contrast, Darrow (1947:345-350) believed control of predators could not be depended upon to result in a continued increase among breeding populations of ruffed grouse (Bonasa umbellus), although control of gray foxes (Urocyon cinereoargenteus), red foxes

(Vulpes vulpes), and weasels (Mustela spp.) produced surpluses of huntable birds in fall. Another study involving ruffed grouse showed no discernible effects from control of predators (Edminster 1939). Robeson et al. (1951) found no appreciable gain in pheasant abundance with control of predators. Hickey's review of the literature (1955) led him to conclude that control of predators was unreliable for increasing populations of gallinaceous birds.

It is apparent a dichotomy exists in results from experiments on control of predators. These differences in results cannot be adequately resolved within existing theory on predation. We hypothesized that habitat pattern and/or structure may influence the rate of predation on ring-necked pheasants (Phasianus colchicus) nests and, by inference, may be able to control the population and therefore could be viewed as a density-independent factor.

The goal of this study was to investigate one aspect of the theory that variations in habitat may affect the rate and action of predation. The objective of this study was to determine if habitat pattern (strip and block) and vegetation structure (% cover by life forms and bare ground, and vegetation obstruction) were related to rates of predation on pheasant nests and on artificial nests. Inferential conclusions may be drawn from rates of predation on nests in different habitats that could show the action of predation as a function of habitat, which may help resolve inconsistencies among studies on control of predators.

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STUDY AREA

We released pen-reared pheasant hens on 2 study areas in the Willamette Valley from 1980 to 1983. Baskett Slough, 1050 ha, located 3 km north of Dallas, Polk County, Oregon, included portions of Baskett Slough National Wildlife Refuge (NWR) and adjacent private lands. Major crops were fescue, ryegrass, winter wheat, and spring grains. Luckiamute, 2000 ha, was located along the Luckiamute River, 8 km south of Monmouth, Polk County, Oregon. Winter wheat, pasture, ryegrass, and corn were the primary crops.

An artificial nest study was used to test for differences in rates of predation between strip and block habitats where habitat structure and density of nests were similar. The artificial nest study was conducted at W. L. Finley NWR, 20 km south of Corvallis, Benton County, Oregon. Test plots were located in grassland/shrub cover adjacent to ryegrass, woodlands, or roads (Fig. 1).

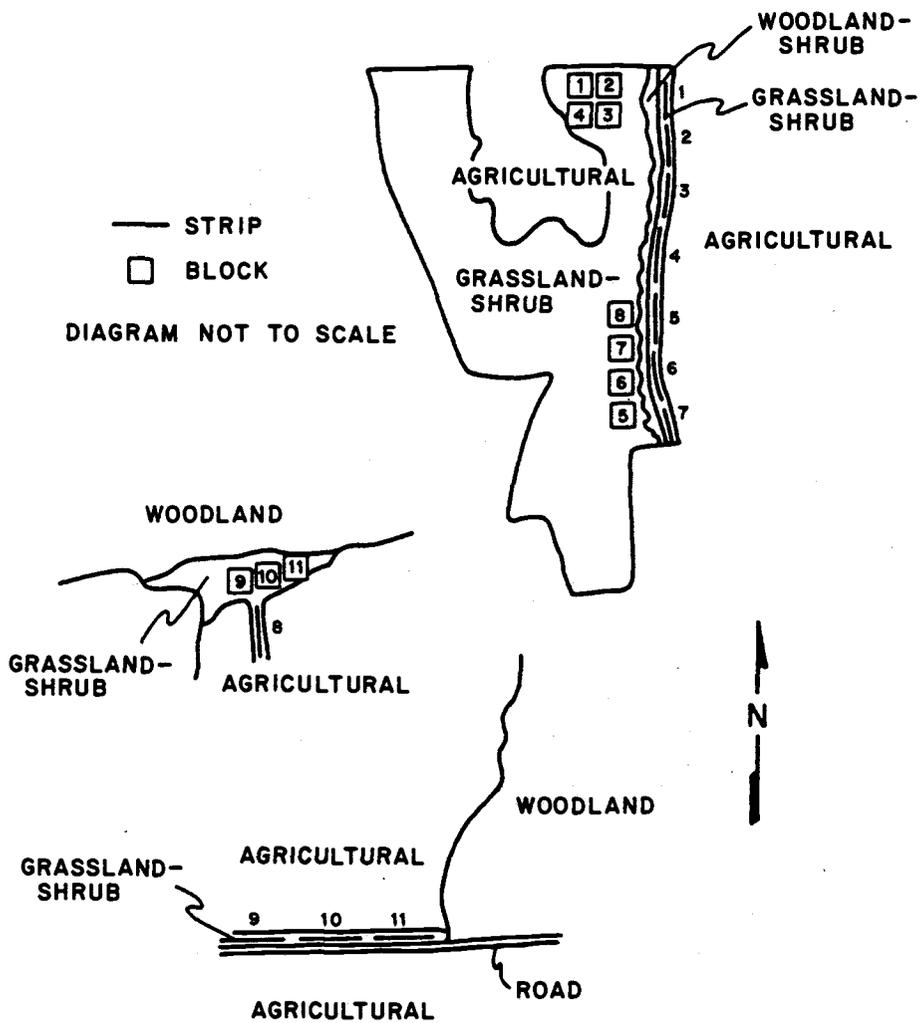


Fig. 1. Location of artificial nest plots at W. L. Finley NWR, Benton Co., Oregon, 1983.

METHODS

Pheasant Hens

We equipped hens with radio-transmitters weighing approximately 27 g (Teleonics Inc., Mesa, Ariz.); transmitters had an operational life of 4-5 months. We attached transmitters to hens with a teflon harness (Bally Ribbon Mills, Bally, Pa.) by a modification of the procedure described by Brander (1968); additional details are found in Meyers (1983). Transmitters recovered from mortalities that occurred during the first few days after release were used in subsequent releases.

Hens were released in groups at 7-14 day intervals from mid-April to mid-May. We released 40, 112, 176, and 140 hens in 1980, 1981, 1982, and 1983 respectively. All birds in 1980 were released at Baskett Slough. We divided birds equally between study areas in 1981-82. In 1983, 84 birds were released at Baskett Slough and 56 were released at Luckiamute. Birds were released throughout each study area. Hens were located within 3 days after release and once weekly thereafter to determine selection of nest sites and fates of nests. Nests were marked with flagging tape at points 2-10 m away from the nest. Fate of each nest was recorded as successful (at least one egg hatched), depredated, or other (abandoned, destroyed by farming, failure due to death of hen, and infertile). Monitoring was terminated 110 days after release.

Predators

Populations of predators were monitored by observation. In addition, raptor nests and red fox dens were located when transmitters were deposited at those sites. There were 10-15 active nests of large raptors and 1-2 active red fox dens each year on Baskett Slough and Luckiamute. Raccoons (Procyon lotor), skunks (Mephitis mephitis), and opossums (Didelphus virginiana) also were present on study areas. We detected no major changes in numbers of predators during the study.

Vegetation Analysis

Structural components of vegetation were measured after hatching or loss of nests. A 0.1-m² circular sampling frame was used to estimate proportion of cover at nest sites for life forms and bare ground immediately adjacent and 5 m from nests along 4 5-m transects. Life forms (modified from Crawford 1974:17) included: a) short grass (<60 cm), b) tall grass (>60 cm), c) forbs, and d) litter (standing dead and down dead material). Transect directions were determined by random compass bearings. The line-intercept method (Mueller-Dombois and Ellenberg 1974:90-92) was used to determine proportion of cover for trees and shrubs in 1980-81. Visual estimates of cover were made in 1982-83 for trees and shrubs around nests from 0 to 1 m and 1 to 5 m. Vertical structure was determined with a cover board (Nudds 1977) in 1982-83 at nest sites along the four transects. Vertical structure variables at 25-50 cm, 75-100 cm, 125-150 cm, and 175-200 cm

were not used in analyses because of significant intercorrelations with other vertical structure variables ($\underline{r} > 0.7$, $\underline{P} < 0.01$). Nest site habitats were classified as strips or blocks. Strip habitats were 1-7 m in width and at least 15 m in length. Strips generally were fencerows, roadsides, and ditch banks. Remaining habitats were categorized as blocks and usually were agricultural fields or wooded-grassland areas.

We defined boundaries for study areas by peripheral locations of hens released in 1981. Composition and acreages of available habitats were determined from aerial photographs. We established random transects, 30-m long, in cover types of habitats to measure structural components. A 0.1-m² circular sampling frame was placed at 10-m intervals along transects to estimate proportion of cover for life forms and bare ground. The line intercept method was employed for trees and shrubs.

Selection indices were calculated for habitats and structural components of vegetation at nest sites. The following formula (VanDyne and Heady 1965:485) was used:

$$SI = \frac{\% \text{ habitat or structural component selected by hens}}{\% \text{ habitat or structural component available to hens}}$$

where $SI < 1$ indicates selection less than occurrence on study area, $SI = 1$ indicates selection equal to occurrence on study area, and $SI > 1$ indicates selection greater than occurrence on study area. Sample sizes for determining available structural components were

calculated from the following formula (Snedecor and Cochran 1980:441-443):

$$\underline{N} = \frac{t^2 s^2}{\underline{\pm} 0.2 \underline{x}}$$

where \underline{N} is sample size, \underline{t} is Student's \underline{t} value at the selected confidence level, \underline{s}^2 is sample variance, and \underline{x} is sample mean.

Artificial Nests

We established 11 block and 11 strip plots of similar vegetative composition (Fig. 1). Each plot contained nine nests of four eggs each. Nests in strips were 23 m apart and centered in each strip; average width of strips was 6 m. Nests in blocks were 18 m apart on a 3 x 3 grid. Density of nests in strips and blocks was approximately 70/ha. Nests were marked with paired flags, 3-5 m on opposite sides of each nest. We established nests on 28 May and checked them once/5 days for 20 days. The testing period was approximately 3 days less than average time of incubation for pheasant nests but with longer periods of exposure, predation can be influenced by egg spoilage (Hammond 1969:4). Hammond (1969:4) stated most predation on artificial nests can be expected within 2-3 weeks after exposure. This test was conducted from 15 April to 17 June 1983.

Statistical Analysis

Comparisons of structural components at nest sites were made with a one-way analysis of variance (ANOVA) program from SPSS (Nie et al.

1975:422-433); means were separated with Duncan's Multiple Range Test (Nie et al. 1975:426-428). Vegetative data collected as proportional values were transformed with the arc-sin transformation (Sokal and Rohlf 1981:427-428). Chi-square tests were used to test for differences in nest fates among periods of initiation and between habitat patterns. A t-test was used to determine if there was a difference in rates of depredation between habitat patterns for artificial nests. Correlations between structural components were analyzed with SPSS (Nie et al. 1975:280-288). Shannon-Weaver functions were determined to assess structural diversity (Hair 1980:273). Mean values of seven structural components (short grass, tall grass, forbs, litter, bare ground, shrub cover, and tree cover) from nests in each habitat were used to compute diversity functions.

RESULTS

Hens released at Baskett Slough and Luckiamute initiated 13, 53, 82, and 76 nests from 1980 through 1983, respectively. Nests from all years were combined for analyses; 17 nests were completely excluded from analyses and 26 were excluded from comparisons of structural components because nests were disrupted prior to completion of vegetation sampling. Vertical structure data were only obtained for nests in 1982-83 ($N = 145$): Dates of initiation were known for 205 nests.

Available Habitat

Grain fields were the dominant cover type (37%) available for nesting. Remaining nesting habitat consisted of 13% seed grass, 19% wooded/grassland, 28% miscellaneous agricultural crops, and 3% strip habitat. Approximately 2% of Baskett Slough and Luckiamute was impoundments, buildings, and farm yards. Structural components available for nesting were 19% short grass, 21% tall grass, 11% forbs, 19% litter, 30% bare ground, 6% shrub cover, and 11% tree cover.

Plots for artificial nests consisted of approximately 30-40% grasses and 25-50% residual herbaceous material. Some forbs (10-20%) and shrubs (0-10%) also were present. Maximum vegetative height ranged from approximately 80-100 cm.

Selection of Nest Sites by Pheasant Hens

Strip habitats were utilized heavily for nesting during the entire season (Table 1). Baskett (1947), Baxter and Wolfe

Table 1. Indices to selection of nest sites by pheasants for habitat patterns and structural components by period of nest initiation, Polk Co., Oregon, 1980-83.

Category ^b	Selection indices ^a by period of nest initiation			
	April	May	June	July/August
Habitat Pattern				
Strip	10.3 (13) ^c	5.7 (15)	7.7 (13)	8.3 (5)
Block	0.7 (29)	0.9 (72)	0.8 (43)	0.8 (15)
Structural Component				
Short grass	1.2	0.8	0.8	0.9
Tall grass	1.2	1.0	0.7	0.5
Forbs	1.2	1.0	1.3	0.9
Litter	1.2	1.2	1.4	1.8
Bare Ground	0.6	1.0	1.0	0.9
Shrub	0.5	0.3	0.3	0.3
Tree	0	0.1	0.5	0.1

^a > 1 = selection for, 1 = neutral, < 1 = selection against.

^b The amount of each habitat pattern and structural component available was adjusted to reflect the entire nesting season including changes resulting from cultivation.

^c Number of nests.

(1973:14-15), and Trautman (1982:47-51) reported similar selection for strips. Block habitats were selected less than they occurred throughout the nesting season (Table 1). There was no change ($P > 0.05$) in frequency of occurrence of nests in strip and block habitats during the nesting season.

Selection indices for tall grass showed a declining trend from April through August (Table 1). Selection indices for litter, the only structural component selected by hens during the entire nesting period, increased through the season. Hens selected bare ground less frequently than it occurred in April and July/August, but selection was neutral during May and June. Shrubs and trees were selected less than their occurrence at all times. Tall grass decreased from means of 24 and 22% at nest sites in April and May to 14 and 10% in June and July/August ($P < 0.01$). Mean percentages of other structural components were not different ($P > 0.05$) among periods of nest initiation (Table 2).

Habitat Pattern and Structure

Significantly ($P < 0.01$) more nests were depredated in strips (53%, $N = 25$) than in blocks (14%, $N = 22$). In addition, nests in strips only had 28% ($N = 13$) success whereas nests in blocks had 49% ($N = 78$) success. Rate of loss of nests to other factors was 19% ($N = 9$) in strips and 38% ($N = 60$) in blocks. Nest success in strips was within the range of results calculated from other studies: 15% (Gates et al. 1970:9), 31% (Dumke and Pils 1979), 37% (Eklund 1942). The rate of nest success for nest in blocks was relatively high compared

Table 2. Vegetative cover at pheasant nest sites by period of initiation, Polk Co., Oregon, 1980-83.

Structural Component	% cover at nest sites by period of initiation			
	April (<u>N</u> =36)	May (<u>N</u> =76)	June (<u>N</u> =51)	July/August (<u>N</u> =18)
Short grass	22	16	16	19
Tall grass	24 AC ^a	22 BD	14 AB	10 CD
Forbs	13	11	13	10
Litter	21	24	27	35
Bare Ground	20	27	31	27
Shrub	3	2	2	2
Tree	<1	1	1	1

^a Means in same row sharing identical capital letters differ ($P < 0.05$, Duncan's Multiple Range Test).

to that calculated from previous research: 26% (Gates and Hale 1975:35), 27% (Baskett 1947), 31% (Dumke and Pils 1979).

We found no significant difference in fates of nests in relation to periods of nest initiation (Table 3). Nesting success ranged from 34% in April to 49% in June. Rates of predation were fairly constant, with the highest rate in April (27%) and lowest rate in May (21%).

Differences in rates of predation between pheasant nests in strips and blocks may have been compounded by differences in habitat pattern and nest density. Density of nests in strips was approximately 53 nests/100 ha. There were approximately 6 nests/100 ha in blocks. Density of nests was constant between strips and blocks in our tests with artificial nests, thus avoiding variability in rates of predation due to interactions of nest density and habitat pattern. Of 99 artificial nests in strips, 36 were depredated; 20% of these losses occurred within 5 days and 50% were destroyed by day 10. Number of nests depredated ranged from 0-7/plot and averaged 3.3/plot. Significantly fewer artificial nests ($P < 0.01$), five, were depredated in block habitats, an average of 0.5/plot.

Pheasant nests in strips had significantly more forbs, litter, and shrub cover than nests in blocks habitats (Table 4). Nests in strips also had more vertical structure at 150-175 cm but less at 0-25 cm. Strips had an index of structural diversity of 1.70, which was similar to that for block habitats, 1.67.

Comparisons were made among pheasant nests grouped by habitat pattern and fate to determine the influence of structural components

Table 3. Fates of pheasant nests by period of nest initiation, Polk Co., Oregon, 1980-83.

Fate	% of nests by period of initiation			
	April	May	June	July/August
Successful ^a	34 (14) ^b	47 (41)	49 (27)	40 (8)
Depredated ^a	27 (11)	21 (18)	23 (13)	25 (5)
Other ^{ac}	39 (17)	32 (28)	28 (16)	35 (7)

^a No significant difference among periods of initiation.

^b Number of nests.

^c Abandoned, destroyed by farming, failure due to death of hen, and infertile.

Table 4. Vegetative cover at pheasant nest sites in strip and block habitats, Polk Co., Oregon, 1980-83.

Structural component	% cover at nest sites by habitat pattern			
	Strip ($\underline{N}^a = 42,27$)		Block ($\underline{N} = 139,118$)	
	\bar{x}	SE	\bar{x}	SE
Short grass	17	2.3	18	1.9
Tall grass	15	2.4	20	1.7
Forbs* ^b	16	2.3	11	1.5
Litter**	34	2.6	23	1.6
Bare ground	19	2.2	29	2.1
Shrub**	4	0.9	2	0.5
Tree	1	0.3	1	0.4
V.O. ^c 150-175 cm*	3	1.5	1	0.6
V.O. 100-125 cm	6	1.9	4	0.8
V.O. 50- 75 cm	27	3.6	34	2.5
V.O. 0- 25 cm**	75	3.1	92	1.2

^a Sample size for 1st 7 and last 4 structural components.

^b * $\underline{p} < 0.05$; ** $\underline{p} < 0.01$.

^c Vegetation obstruction.

Table 5. Vegetative cover at pheasant nest sites by habitat pattern and fate, Polk Co., Oregon, 1980-83.

Structural Components	% cover at nest sites by habitat pattern and fate							
	Strip				Block			
	Successful ($N^a = 13,8$)		Depredated ($N = 23,15$)		Successful ($N = 71,60$)		Depredated ($N = 21, 15$)	
	\bar{x}	SE	\bar{x}	SE	\bar{x}	SE	\bar{x}	SE
Short grass	11	2.5	20	3.6	13	2.4	18	4.5
Tall grass	23	6.2	12	2.0	23	2.3	21	5.0
Forbs* ^b	16 A ^c	5.2	15 B	2.7	9 AB	1.6	11	2.7
Litter*	27	4.4	37 AB	3.6	24 A	2.6	23 B	4.1
Bare ground	24	4.6	16	2.6	31	3.1	27	5.6
Shrub**	3	1.2	4 AB	1.4	2 A	0.8	1 B	0.5
Tree	1	1.1	<1	0.3	1	0.7	1	0.5
V.O. ^d 150-175 cm*	6 AB	4.7	2	0.8	1 A	0.9	1 B	0.7
V.O. 100-125 cm	10	5.4	5	1.8	5	1.2	4	0.8
V.O. 50- 75 cm	32	7.3	26	4.0	38	3.4	33	7.4
V.O. 0- 25 cm**	76 AB	6.0	77 CD	3.9	93 AC	1.6	91 BD	2.9

^a Sample size for 1st 7 and last 4 structural components.

^b * $P < 0.05$; ** $P < 0.01$.

^c Means in same row sharing identical capital letters differ ($P < 0.05$, Duncan's Multiple Range Test).

^d Vegetation obstruction.

on fates of nests (Table 5). Forbs, litter, shrub cover, vertical structure at 150-175 cm, and vertical structure at 0-25 cm were significantly different. Successful nests in block habitats had less forb cover than all nests in strips. There was more litter and shrub cover at depredated nests in strips than all nests in blocks. Vegetation obstruction at 150-175 cm was greater at successful nests in strips than all nests in blocks. All nests in strips had less vegetation obstruction at 0-25 cm than all nests in blocks. Structural components could not be used to differentiate successful and depredated nests in either strips or blocks.

Apparently, fates of nests were influenced more strongly by habitat pattern than structural components at nest sites. Horkel et al. (1978) concluded vegetation types did not influence rates of predation on artificial nests. Byers (1974) found artificial nests with deeper litter, denser cover, and greater vegetative height were not more successful. By contrast, Wray and Whitmore (1979) found differences in structural characteristics between successful and unsuccessful nests.

DISCUSSION

Pheasant hens strongly selected strip habitats for nesting; concentrations of nests in strips were nearly 9 times greater than in blocks. Nests in strips had rates of predation 4-7 times greater than nests in blocks, both from pheasant nests where densities were greater in strips and from artificial nests where densities were similar in strips and blocks. We found differences in vegetative structural components between nests in strips and blocks, but no differences between successful and depredated nests within either habitat pattern. We concluded rates of predation on nests were primarily a function of habitat pattern.

Interactions of habitat characteristics may create conditions that drastically increase vulnerability of nests. Studies by Chesness et al. (1968), Duebbert and Kantrud (1974), and Bowman and Harris (1980) indicated vulnerability of nests was associated with structural characteristics at nest sites. Chesness et al. (1968) found a 10% increase in nesting success for pheasants on areas with control of predators, but in different habitats rates of predation ranged from 4 to 64%. Levels of predation decreased as concealment quality of cover increased. Rates of predation were greatest in strip habitats (e.g. fencerows, ditches) both where predators were controlled and left undisturbed. Duebbert and Kantrud (1974) found that blocks of grassland with tall, rank cover in areas without reduction of predators had significantly higher production of waterfowl than areas of less cover with control of predators. They suggested control of

predators would not result in greatly increased production in areas lacking abundant nesting cover. Bowman and Harris (1980) found depredation of artificial nests decreased on areas where vegetation density and complexity were increased or maintained regardless of density of nests. They also found that the level of nest concealment did not influence depredation of nests, except when nests were in the open and predators had abundant search time. They found numbers of clutches located by predators decreased with increased vegetative heterogeneity and concluded managing for increased spatial heterogeneity may be useful in increasing density of nests and nest success for ground-dwelling birds. In contrast, results from our study indicated vulnerability of nests was primarily associated with habitat pattern.

Increased vulnerability of nests may in part reflect increased exposure to predators. Strips and edges have been indentified as biological barriers (Bider 1968) and travel lanes for predators (Chesness et al. 1968, Leopold 1977). Gates and Gysel (1978) and Horkel et al. (1978) reported activities of predators were greater around habitat discontinuities (e.g. rights-of-ways, fencerows). Chasko and Gates (1982) and Rodenhouse and Best (1983) found rates of depredation decreased as distance from habitat edges increased.

Predators may also be more effective in finding prey in strips, especially where prey are concentrated. The impact of predation may be especially great for species of prey that strongly select strips for nesting. The combination of concentrated numbers of prey and

increased efficiency of predators may create conditions in which predation could be density-independent.

It is likely that at some point with increasing width of strips, vulnerability of nests could be drastically reduced because of a decrease in the ability of predators to locate nests, thereby shifting predation back to a density-dependent action. Hamerstrom (1936) and Gates and Hale (1975:37) reported wider strips had higher rates of nest success and suggested width of strips may be a factor in nest success. The point at which a change in the action of predation occurred would probably involve a dynamic balance of structural heterogeneity, distribution of habitats, degree of concentration of prey, and size of predator and prey populations. Narrow strips can be insecure even with high structural heterogeneity. Strips may be secure though, if there was a sufficient number and distribution of these habitats. In effect, a large number of strips in relation to populations of predators may cause predation to act in a density-dependent manner.

Other types of habitats where prey are concentrated may indicate areas in which predation might also become density-independent. Corsi (1973) stated that programs for leasing small acreages in farming areas had little impact on abundance of pheasants because of insufficient acreage and distribution of habitats. Failure of these programs may have resulted from density-independent predation, which depressed populations of pheasants. Bowman and Harris (1980) hypothesized that where structural heterogeneity was increased by establishing a relatively few small patches, predators might soon

learn to exploit prey in those areas. Jackson et al. (1975:23) speculated that with declines in suitable pheasant habitat, efficiency of predators had increased because the few remaining non-cultivated areas (e. g. fencerows, road ditches, shelter belts) could be covered more thoroughly.

It is apparent from our data and previous research that rates of predation are associated with prey habitat, and habitat pattern and structural characteristics may influence vulnerability of prey. In habitats such as strips where prey can be concentrated and effectiveness of predators can be high, predation may become density-independent. By viewing predation as having the capacity to act in a density-independent fashion in some habitats, differences among predator control experiments can be more easily understood.

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