CHAPTER TWO

Mechanistic Approaches to the Investigation of Edge Effects on Avian Productivity

ABSTRACT

In recent decades researchers and land managers have focused much attention on the influence of edges on avian nest success. Studies have been conducted in many different systems to determine if the presence of ecotones serves to elevate levels of nest predation and brood parasitism and thereby reduce breeding success. There has been, however, surprisingly little attention given to understanding the mechanisms involved in these edge effects, and there is not therefore a clear understanding of why edge effects occur in some situations and why they do not in others. Gates and Gysel (1978) proposed that elevated nest densities in the vicinity of ecotones attract predators and brood-parasitic Brown-headed Cowbirds. It is not clear, however, that such a mechanism would increase the proportions of nests depredated or the proportions of nests parasitized. Here I develop models of the interrelationships among distance to edge, cowbird density, host density, and level of parasitism. This theoretical framework suggests that it is unlikely that the level of parasitism would increase in

response to elevated nest densities unless cowbirds respond both functionally and numerically to host density. I describe an approach to investigate empirically the relationships among these variables.

Much of this chapter is published elsewhere (Winslow 1999).

POPULATION DECLINES IN NEOTROPICAL MIGRANT BIRDS

Data from the North American Breeding Bird Survey indicate that a number of species of Neotropical migrant birds have experienced population declines in recent decades (Sauer and Droege 1992, Peterjohn *et al*. 1995). It is unclear whether this represents a general phenomenon, since there are other species of Neotropical migrants that have increased in number over the past few decades (James and McCulloch 1995, James *et al*. 1996). It is difficult to ascertain the causes of declines for any species of Neotropical migrant, since explanations may involve factors that operate in any of the three components of these species' ranges: breeding (e.g. Sherry and Holmes 1992, Böhning-Gaese *et al*. 1993), wintering (e.g. Rappole and McDonald 1994), and migratory stopovers (e.g. Moore and Simons 1992). This dissertation focuses on factors that may operate on the breeding grounds.

Breeding productivity, and thus population dynamics, of

Neotropical migrants may be affected by both the loss (decrease in total area) and fragmentation (decrease in contiguity) of breeding habitat.

DIRECT EFFECTS OF HABITAT LOSS

Decreased availability of habitat should decrease the number of breeding territories and thus directly reduce population-level productivity. The extent to which productivity is reduced will depend in part on the relationships among habitat availability, population density, territory size, and individual productivity (Fretwell 1972, Hixon 1980). Individuals whose territories are destroyed as a result of habitat loss will be displaced. Such individuals may attempt to breed somewhere within adjacent habitat, or may seek suitable habitat elsewhere.

If displaced individuals attempt to breed in nearby habitat, breeding density may increase and territory size may decrease. Decreased territory size may not fully compensate for the loss of habitat, since territory size is unlikely to increase in proportion to area lost indefinitely (Huxley 1934, Zimmerman 1971, Fretwell 1972, Hixon 1980). In addition, a decrease in individual productivity with decreasing territory size may further reduce population-level productivity (Zimmerman 1971). Components of productivity which may decrease with decreasing territory size include pairing success, number of mates, clutch size, nestling growth and development, and number of broods attempted.

Alternatively, breeding density may remain constant if displaced individuals (or inferior competitors in the area) seek suitable habitat elsewhere or if recruitment to the local breeding population is reduced. In such cases, population-level productivity may decrease in direct proportion to the loss of habitat.

EDGE EFFECTS

Faunal community composition, as well as densities and activity patterns of individual species, may change clinally with proximity of breeding habitat to ecotones. In this chapter the term *edge effect* refers generally to any such spatial gradient. Edge effects may involve increases in avian breeding density near edges, as well as increases in the abundance and activity patterns of nest predators and brood parasites (Wilcove, 1985; Ambuel and Temple, 1983; Brittingham and Temple, 1983; Chasko and Gates, 1982; Whitcomb *et al.*, 1981; Gates and Gysel, 1978). Over the past two decades ornithologists have conducted a great number of field studies to investigate edge effects on avian productivity, but there has been relatively little discussion of the mechanisms that may cause such effects.

Gates and Gysel (1978) presented avian reproductive data from three study sites in southern Michigan, each containing forest and field habitats adjacent to one another. They found that nest density was higher along the forest-field edges than in interior forest or field habitats. They also found that the incidences of nest predation and brood parasitism were higher along the ecotone, and they attributed these results to *functional responses* (Holling, 1959) of nest predators and parasitic Brown-headed Cowbirds (*Molothrus ater*) to the increased availability of nests in the edge habitats. Since that time there have been many investigations of edge effects in very different systems and on different continents, but discussion of the functional responses proposed by Gates and Gysel has been largely neglected.

Paton (1994) reviewed the evidence for edge effects of nest predation and of brood parasitism by Brown-headed Cowbirds. He found that most studies have shown edge effects, but that many have not. Ten of 14 studies of artificial nests and four of seven studies of natural nests showed decreasing incidence of predation with increasing distance from edge, while three of five studies of natural nests showed decreasing brood parasitism with increasing distance to edge. He concluded that edge effects occur within 50 m of an edge, but that evidence for effects over greater distances is unconvincing. Thus it appears that edge effects may occur in some situations, but it is not clear why.

Although many published studies have attempted to test hypotheses about edge effects on avian breeding density and success, little attention has been given to understanding the mechanisms underlying these effects. For this reason, it is not readily apparent why, when, where, or whether we should expect edge effects to occur. Furthermore, evaluation of edge-effect hypotheses is not necessarily straightforward when both breeding density and nesting success may vary with distance to edge. There is thus a great need for investigators to develop mechanistic approaches.

It is the purpose of this chapter to investigate conceptually possible mechanisms that may cause edge effects. I develop simple analytic models to describe brood parasitism by Brown-headed Cowbirds in the forests of eastern North America. By considering how these models work together, I describe a series of possible mechanisms by which edge effects may occur. I explain how the qualitative and quantitative assumptions and predictions of each mechanism can be tested to evaluate (1) whether edge effects occur in a given situation, and (2) which mechanisms operate to produce edge effects in various systems.

It should be possible to extend this framework to address similar phenomena involving nest predation and to describe edge effects of nest predation or of other species interactions in other ecosystems or regions. When appropriate I discuss how proposed mechanisms are relevant to nest predation, but I restrict formal modeling to cowbird parasitism in this contribution.

I use this theoretical framework, in the context of cowbird parasitism, to address the following questions: (1) What mechanisms might explain edge effects? (2) What are appropriate null models against which apparent edge-effect patterns should be tested? (3) What alternative (edge-effect) models should be tested against these null models in order to determine whether edge effects occur? (4) What quantitative and qualitative predictions follow from each model? (5) How can we test assumptions and predictions of each model? (6) How can proposed mechanisms be understood in terms of a framework of analytic models? (7) How can we test assumptions and predictions of proposed mechanisms of edge effects? I hope that we may eventually gain the understanding to predict the occurrence and magnitude of edge effects in various ecological communities.

MECHANISMS OF EDGE EFFECTS

There are several possible mechanisms by which proximity to an ecotone may influence avian breeding success. Here I discuss null models based on variation in nest density and also more complex models that incorporate *functional* and *numerical responses* (Holling, 1959) of nest predators and brood parasites to gradients (spatial or temporal) in nest density. Mechanisms that may explain elevated levels of cowbird parasitism and nest predation near edges include (1) functional responses to elevated nest density based on increased encounter rates and/or search facilitation; (2) variation in avian community composition as a function of habitat or of context within a landscape; (3) functional responses to nest density involving spatial patterns of activity of predators or cowbirds within their home ranges ("*pseudo-numerical responses*"); (4) activity patterns of predators or cowbirds directly influenced by the presence of edge habitat ("*structure-directed responses*"); (5) activity patterns of predators or cowbirds influenced by the adjacent habitat (e.g., attraction of cowbirds to snags within forest disturbances); (6) numerical responses (immigration or increased reproductive success) of nest predators or cowbirds to nest density; and (7) alterations in vegetative structure near edges that facilitate the searching behavior of cowbirds or predators.

A. Null Models Based on Nest Density

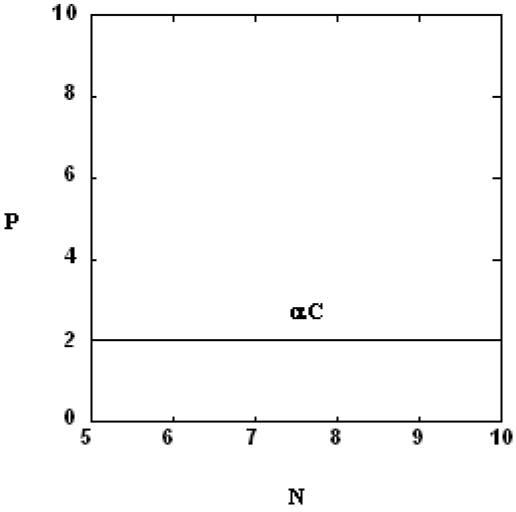
Nest density may be elevated near an edge, because an increased number of species breed in ecotonal habitat (Gates and Gysel, 1978). In the absence of any functional or numerical responses of predators or cowbirds, increased nest density should be associated with lowered proportions of nests preyed upon and parasitized (Fretwell, 1977; Clark and Robertson, 1979). *Level of parasitism* by Brown-headed Cowbirds has, in fact, been shown to vary inversely with nest density in Yellow Warblers (*Dendroica petechia*, Clark and Robertson, 1979), Dickcissels (*Spiza americana*, Zimmerman, 1983; Fretwell, 1977), and Red-winged Blackbirds (*Agelaius phoeniceus*, Freeman *et al*., 1990; Orians *et al*., 1989; Fretwell, 1977). Accordingly, attempts to detect numerical or functional responses of nest predators or brood parasites to elevated nest densities along edges should employ appropriate null models that account for this "swamping" effect.

For example, consider cowbird parasitism over a nest density gradient where cowbirds do not vary in number or activity patterns. In order to parasitize a nest, a female cowbird must lay her egg during the laying stage or early in the incubation of the host nest. At a high enough nest density cowbirds may be limited by the rate at which they can lay eggs, as opposed to the rate at which they can find available host nests. If this is the case (or if search time does not vary with nest density), there will be no functional response of parasitism to host density. The number of eggs laid in host nests by each female cowbird will remain constant, and the *level of parasitism* (which may be measured as mean number of cowbird eggs per host nest) will decrease with increasing nest density. This null model may be expressed by the equation

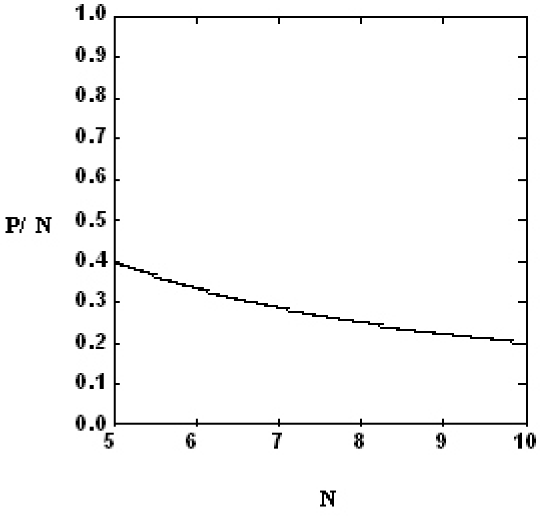
$$P=\alpha C, \qquad (1)$$

where P is the temporal rate at which cowbird eggs are laid in nests of all host species per unit area, α is the maximum rate of egg production per female cowbird, and C is the density of breeding female cowbirds (Figure 2.1.a, b). I refer to this as the "egg limitation model."

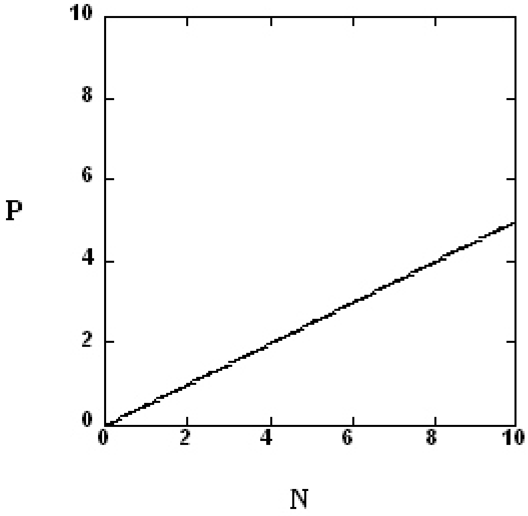
A similar model will apply to situations where parasitism is limited by the rate at which cowbirds find nests and search time does not decrease with increasing nest density. This relationship is expressed as


P
N
αC
0
2
4
6
8
10
5
6
7
8
9
10

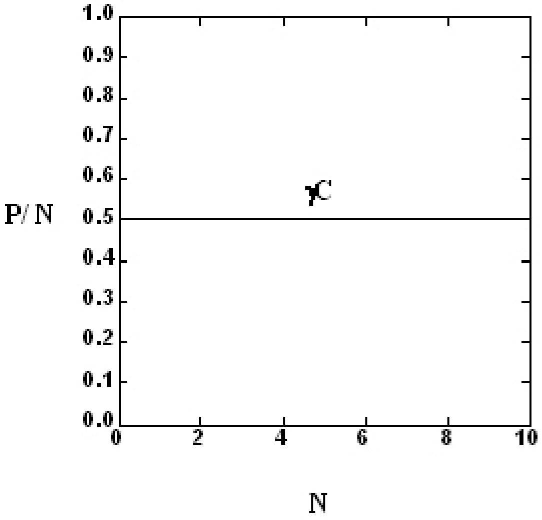
a.


P/ N
N
1.0
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0.0
5
6
7
8
9
10

b.


P
N
0
2
4
6
8
10
0
2
4
6
8
10

c.


P/ N
N
γC
1.0
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0.0
0
2
4
6
8
10

d.

Figure 2.1: (a.) Null model of brood parasitism ($P = \alpha C$). P is the rate per unit area at which cowbird eggs are laid in host nests, α is the rate at which female cowbirds produce eggs, and C is the density of female cowbirds. The x-axis denotes N, the rate per unit area at which host nests become available for parasitism. Under the null model, P is assumed not to vary with N. (b.) Level of parasitism as a function of nest availability under the null model. The *level of parasitism* (P/N) decreases with increasing N. The level of parasitism as here defined may be measured as the number of cowbird eggs per nest (including both parasitized and unparasitized nests) over time intervals in which P and N are constant. (c.) The encounter-rate limitation model of brood parasitism ($P = \gamma NC$). The parameter γ is the average rate (per cowbird) at which an individual female locates available host nests per unit of nest availability. (d.) Level of parasitism as a function of nest availability under the encounter-rate limitation model. The level of parasitism (P/N) remains constant with increasing N.

$$P = \beta C,$$

where β is the average rate at which a female cowbird locates nests. This "search-time limitation model" is appropriate for a situation in which cowbirds find most nests by observing the behavior of hosts (Norman and Robertson, 1975; Hann, 1941). For parasitism to be limited by the rate at which cowbirds find nests, I assume that a cowbird prefers to lay only one egg per nest, although any nest may be parasitized by more than one female (Lyon, 1997; Smith and Arcese, 1994). For this reason, at sufficiently low nest densities cowbirds will be limited by the availability of nests to parasitize.

Under the search-time limitation model, as in the egg limitation model, there is no functional response of parasitism to nest density, and parasitism level therefore decreases with increasing *nest availability*. Accordingly, if nest density rises near an edge, there should be, in the absence of functional or numerical responses of cowbirds, a lower level of parasitism near the edge than at greater distances. This pattern, if detected in a field study, might be interpreted as an edge effect, although one opposite in direction from the trends often described. If the variable of interest is P, however, this lower parasitism level should be regarded not as an edge effect but rather as the absence of an edge effect. This point underscores the importance of choosing the correct null model.

B. Functional Responses of Encounter Rate

I now instead assume that female cowbirds are limited by the rate at which they can find nests to parasitize, and that this rate is proportional to *nest availability* (rectilinear functional response, Holling, 1959). This situation may occur, for instance, if cowbirds encounter nests through systematic searching, and higher nest densities lead to higher encounter rates. This relationship (the "encounter-rate limitation model") can be expressed as

$$P=\gamma NC, \qquad (2)$$

where N is the rate at which host nests become available per unit area and γ is the average rate (per cowbird) at which an individual female locates available host nests per unit of nest availability (Figure 2.1.c).

Since Brown-headed Cowbirds are obligate brood parasites, a rectilinear functional response seems appropriate when considering the density of all available host nests. This model implicitly assumes that each cowbird successfully parasitizes each nest she encounters, i.e., that she is able to lay an egg and it is not removed by the hosts. This model also assumes no cowbird lays more than one egg in the same nest but that nests may be parasitized by more than one female. If the density of cowbirds does not vary with N or with time, the model predicts that the *level of parasitism* (P/N) remains constant with changes in N (Figure 2.1.d).

It is important to note that P/N is not equivalent to the number of cowbird eggs per host nest if P or N varies with time. Under the encounter-rate limitation model, the number of cowbird eggs per host nest will not vary with N so long as cowbird density does not vary with N or time. Therefore, if parasitism is limited by encounter rate and cowbird density remains constant, the average number of cowbird eggs per nest should remain constant with changes in nest availability.

Smith and Arcese (1994) present data on cowbird-host dynamics for a population of Song Sparrows (*Melospiza melodia*) on Mandarte Island, British Columbia. In this study the total number of cowbird eggs laid in all sparrow nests within a given year increased in a roughly linear fashion with increases in sparrow density (their Figure 1). They found no increase in proportion of nests parasitized with increasing sparrow density, a result that is consistent with the encounter-rate limitation model. Also, Strausberger (1998) studied parasitism of seven cowbird hosts in edge habitat in northeastern Illinois and presented data consistent with encounter-rate limitation.

A pattern similar in form (see Figure 2.1) to that predicted by the encounter-rate limitation model [Eq. (2)] may also occur if the mean egg production rate of cowbirds varies in proportion to nest density over the course of a breeding season. Fleischer *et al.* (1987) found that the rate of egg production by Brown-headed Cowbirds peaked in mid-season. This may result largely from variation in the proportion of females in reproductive condition rather than from variation in individual laying rates of reproductively active females (Rothstein, *pers. comm.*). In either case, these findings underscore the importance of considering variation in nest availability (N) and the rate per cowbird of egg production (α) over the course of the breeding season.

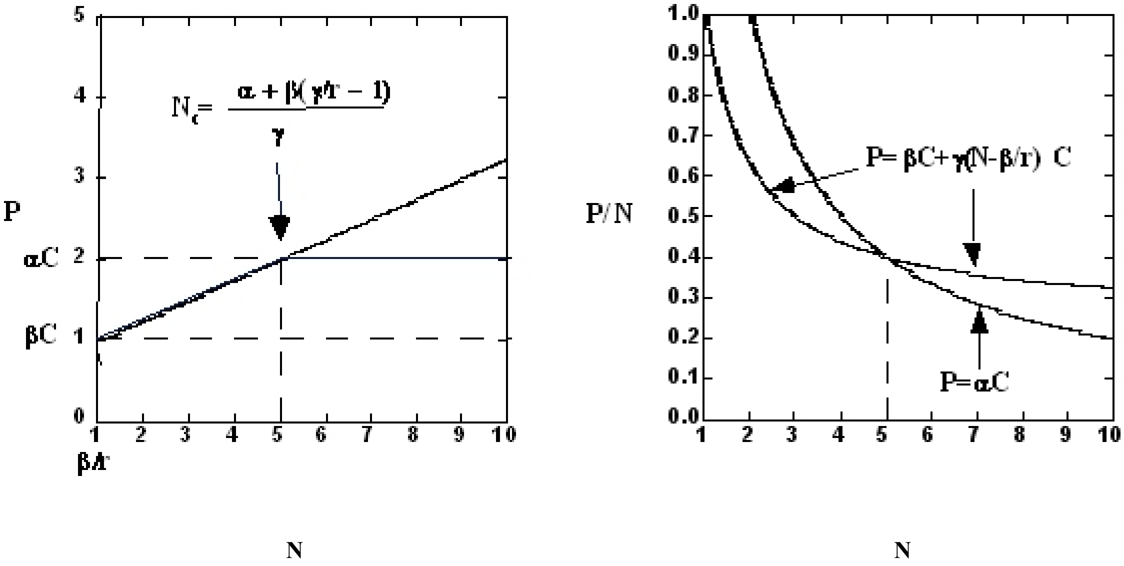
If some proportion of host nests is located through random encounters and another proportion through observation of host behavior, the rate at which cowbird eggs are laid in host nests may be described as

$$P = \beta C + \gamma\left(N - \frac{\beta}{r}\right)C, \qquad (3)$$

for

$$\frac{\beta}{r} \leq N \leq \frac{\alpha + \beta\left(\frac{\gamma}{r} - 1\right)}{\gamma},$$

where r is the mean area of a female cowbird's breeding range. I call this the "finding-rate limitation model" (Figure 2.2.a). The first term on the right-hand side of Eq. (3) represents the component of finding-rate limitation that is independent of changes in N. If $\beta = 0$, this model is equivalent to Eq. (2). The second term on the right-hand side of Eq. (3) represents the component of location-rate



a. **b.**

Figure 2.2: (a.) Finding-rate limitation model of brood parasitism [$P = \beta C + \gamma(N - \beta/r)C$]. The parameter β is the rate at which female cowbirds locate nests through active observation of host parents, r is the mean area of a female cowbird's breeding range, and the other symbols are defined in the caption of Figure 1. This model is assumed to apply when $\beta/r < N < N_c$. When $N > N_c$, the null model $P = \alpha C$ applies. (b.) Level of parasitism as a function of nest availability under the finding-rate limitation model. The level of parasitism decreases with increasing nest availability.

limitation that varies with N (encounter-rate limitation). If $\gamma = 0$, the second term is 0 and this model is equivalent to the search-time limitation model above ($P = \beta C$).

The purpose of the ratio β/r in the second term on the right-hand side of Eq. (3) is to insure that nests discovered by watching hosts (i.e., accounted for by the first term βC) do not figure into the level of nest availability (N) that influences the encounter rate. The finding-rate β is divided by the variable r in order for that term to have the same units as N {nests/(area*time)}. If the breeding home ranges of female cowbirds are fully exclusive (see Section D below), then $r = 1/C$ and Eq. (3) simplifies to $P = \beta C + \gamma NC - \gamma\beta$. Note that in this situation, under model assumptions there is no multiple parasitism.

In temperate forests nest density varies greatly over the course of a breeding season, increasing quickly at the beginning and peaking before the middle of the season. There may be a critical nest availability (rate per unit area of nest initiation),

$$N_c = \frac{\alpha + \beta\left(\frac{\gamma}{r} - 1\right)}{\gamma} = \frac{\alpha}{\gamma} + \frac{\beta}{r} - \frac{\beta}{\gamma},$$

at which further increases in availability do not elicit further functional responses of parasitism (Figure 2.2.a). If so, Eq. (3) may apply at the beginning and the end of the season, and the egg limitation model [Eq. (1)] may apply during the peak of nesting activity. When $N = \beta/r$, cowbirds will be limited by the rate at which nests become available for parasitism ($P = rNC$), and all nests will be parasitized.

Under the finding-rate limitation model, the level of parasitism (*P/N*) decreases with increasing nest availability (Figure 2.2.b). As β approaches 0, this model approaches the encounter-rate limitation model [Eq. (2)], and level of parasitism ceases to vary with nest density. Therefore, in the absence of a numerical response, the level of parasitism of all host species should not increase with increasing nest availability.

Patterns of nest predation may differ from those of cowbird parasitism. Many predators may be facultative with regard to nest predation (Howlett and Stutchbury, 1996; Vickery *et al.*, 1992), relying on other resources when nests are scarce. For this reason, nest predators may exhibit accelerating functional responses to nest density, switching to searching for nests when they are abundant (Holling, 1959). This may lead to increased proportions of nests depredated as nest density increases, even in the absence of a numerical response (see Section D below). For instance, Fretwell (1977) found that predation on Dickcissel nests increased as density of breeding females increased, whereas cowbird parasitism did not (see Section A above). Also, levels of nest predation are often higher during peak nesting than later in the season when some birds have finished breeding (Chapter 3, this volume; Wilson and Cooper, 1998; Nolan, 1978; Gottfried and Thompson, 1978).

It is interesting to note that Smith and Arcese (1994) observed a density-dependent response of increased nest failure with increased Song Sparrow density, although they did not see a similar pattern for cowbird parasitism (see above). They suggest that this pattern of nest failure resulted from increased nest *predation* by Brown-headed Cowbirds, which served to stimulate host renesting (Arcese *et al.*, 1996; Smith and Arcese, 1994; Arcese *et al.*, 1992). It is unclear why the level of cowbird nest predation increased with increasing host density while the level of brood parasitism by cowbirds did not vary with changes in host density. Perhaps this indicates that some degree of "egg limitation" of parasitism exists in this system (Arcese, *pers. comm.*). However, the general pattern indicates encounter-rate limitation, i.e., the total annual number of cowbird eggs laid in all sparrow nests increased in a roughly linear fashion with increases in sparrow density (a "functional response to host density," Smith and Arcese, 1994). Another possibility might be that nest predators exhibited an accelerating functional response; however, data presented by Arcese *et al.* (1996) suggest that predators other than cowbirds did not respond to increased sparrow densities.

These models of functional response to nest availability have implications for the detection of edge effects where nest density varies with distance to an edge. If nest density is higher near an edge, the proportion of nests parasitized or depredated may not vary with distance (or may actually be lower near the edge), even if cowbirds or nest predators respond to the higher density. Thus it is important to contrast models of edge effects with appropriate null models (see Section A). It is also necessary to consider how the community composition of breeding birds varies with distance to edge.

C. Avian Community Composition

This formulation becomes more complex if we consider multiple host species that differ in abundance and in the level at which they are parasitized. Species often vary considerably in parasitism level (e.g., Chapter 1, this volume; Strausberger and Ashley, 1997). This variation may result from differences in one or more of the following: (1) extent of overlap in breeding phenology between cowbirds and their various hosts (e.g., Peer and Bollinger, 1997), (2) preferences of cowbirds for different hosts (e.g., Strausberger and Ashley, 1997; Peer and Bollinger, 1997), (3) variation in host aggressiveness toward cowbirds (e.g., Uyehara and Narins, 1995; Mark and Stutchbury, 1994; Bazin and Sealy, 1993), (4) variation in the facility with which cowbirds can find nests of different species, and (5) egg ejection by hosts, which affects observed levels of parasitism (Strausberger and Ashley, 1997; Rothstein, 1976).

Edge effects of parasitism have often been described by pooling data from nests of all species monitored (e.g., Brittingham and Temple, 1996; 1983; Gates and Gysel, 1978). Such comparisons are likely to be flawed, as samples may differ in species composition and may not accurately represent the structure of the communities from which they are drawn (Bielefeldt and Rosenfield, 1997). Because cowbirds may base their breeding decisions on the availability of nests of preferred hosts, the intensity of parasitism of a single species may also vary with host community composition. For these reasons it is important to consider community structure in order to understand the effects of edge on parasitism.

These considerations may necessitate the development of models that take into account interspecific differences in nest density and concealment, host quality and defense behavior, etc. When parasitism is limited by the rate at which cowbirds find nests, the rate per unit area at which their eggs are laid in nests of species i can be expressed as

$$p_i = f_i g_i h_i C,$$

where f_i is the rate at which an individual cowbird locates nests of species *i*, g_i is the probability that a cowbird will attempt to parasitize a nest of species *i* given that she locates it, and h_i is the probability that a cowbird that attempts to parasitize a nest will succeed (i.e., is not deterred by host aggression and is able to lay an egg that is not ejected). Although there are other defenses hosts employ against parasitism (e.g., nest desertion, damaging cowbird eggs, rebuilding over a parasitized clutch), in such cases an observer is likely to detect the parasitism event. An observer is not likely to detect failure to parasitize as a result of host aggression or egg ejection.

A finding-rate limitation model for an individual host species *i* is

$$p_i = [\beta_i + \gamma_i (n_i - \frac{\beta_i}{r})] g_i h_i C, \tag{4}$$

where n_i is the rate per unit area at which nests of species *i* become available for parasitism, g_i is the average rate per unit of nest availability at which an individual female locates available nests of species *i* by random or systematic searching, and β_i is the rate at which a cowbird finds nests of species *i* by active observation of breeding adults. This rate β_i will vary with host community composition, since it is a function of the amount of time cowbirds devote to searching for nests of each species. If $\beta_i > 0$, then it is presumably adaptive for a cowbird to attempt to parasitize any nest of species *i* she finds; thus $g_i = 1$. If $\beta_i = 0$, an encounter-rate limitation model applies for that host species. If all host species within a community are identical with regard to location rate, encounter rate, and host quality, and if cowbirds always succeed in parasitism attempts, then

$$P=\sum p_i=\beta C+\gamma(N-\frac{\beta}{r})C,$$

which is the finding-rate limitation model for nests of all species discussed above [Eq. (3)]. Thus Eq. (3) is a special case of a more general formulation in which variables such as finding rate may differ among species.

To proceed further in describing how cowbird eggs may be distributed among available host species, it is necessary to understand how cowbirds choose which nests to lay in. Although studies have addressed questions of which hosts are suitable and why certain hosts are avoided (e.g., Pribil and Picman, 1997; Strausberger and Ashley, 1997; Peer and

Bollinger, 1997), it is not well understood how female cowbirds choose among suitable host species in a community (Petit and Petit, 1999).

Certainly, not all breeding decisions appear to be optimal, since cowbirds do lay in nests of rejector species (Rothstein, 1976). Also, Strausberger and Ashley (1997) found that hosts of relatively high quality (measured as probability of nest survival) were not more likely to be parasitized than hosts that were otherwise suitable but of lower quality. In the next paragraphs I will develop a simple model to predict variation in parasitism levels among species, under the assumption that cowbirds make adaptive breeding choices. Although this assumption is not entirely tenable and leads to unrealistic predictions, it may provide a foundation for more complex models that account for variation in host preferences among cowbirds.

We can use an optimal foraging approach to model how the vector of location rates β_i varies with community composition and densities of host species. We use

$$t_i = s_i(\beta_i - \gamma n_i) \tag{5}$$

to denote the proportion of a cowbird's total time available to a cowbird (i.e. 24 hours) that is spent searching for nests of species *i*, where s_i is the time required for a female cowbird to find a nest of species *i* while she is actively searching. The term $-\gamma_i n_i$ reflects the fact that it is unnecessary to search for nests encountered randomly. If cowbirds behave in an adaptive fashion, they should first allocate available searching time to host species with the highest *search payoff* $h_i q_i / s_i$ (assuming a negligible cost of failure to parasitize), where q_i is equal to host quality (measured as cowbird fledglings produced per cowbird egg laid in nests of species *i*). Thus cowbirds should not allocate time to searching for nests of less favorable hosts unless they are able to find all nests of species with the highest search payoffs.

Assuming a cowbird can find and attempt to parasitize all nests of these more favorable species within her breeding home range,

$$t_i = s_i n_i (r - \gamma_i). \qquad (6)$$

Comparing Eqs. (5) and (6), it is apparent that $\beta_i = n_i r$. Assuming that $g_i = 1$ (since it would be adaptive for a cowbird to attempt to parasitize any nest of such a species she encounters) and substituting $n_i r$ for β_i in Eq. (4), the rate at which cowbird eggs are laid in nests of a preferred species is thus

$$p_i = n_i r h_i C,$$

and

$$f_i = \beta_i = n_i r.$$

That is, cowbirds locate nests of such species as fast as they are begun.

In conditions in which each cowbird can find and attempt to parasitize each nest of such a preferred species within her breeding home range, this model predicts that the level of parasitism (p_i/n_i) will not vary with n_i. The level of parasitism for host species with no defense to parasitism (i.e. $h_i = 1$) will be equal to rC, the average number of female cowbirds within whose ranges any nest occurs. If the most preferred species is too numerous for all its nests to be found by any given cowbird, then cowbirds should search only for this species and the following formulation (least favorable species searched for) should apply to parasitism of the most preferred species.

Under the assumption of optimal host choice, any given cowbird will locate some but not all nests of the least favorable of those species searched for. We assume that g_j (the probability that a cowbird will attempt to parasitize a nest of such a least favorable species j given that she finds it) is equal to the probability that an individual cowbird is unable to find and parasitize a nest of a species with a *parasitism payoff* greater than $h_j q_j$ during the time it takes her to produce one cowbird egg. This probability is

$$g_j = \prod \left(1 - \frac{f_k h_k}{\alpha(f_k + 1)} \middle| k \in K\right), \tag{7}$$

where K is the set of species k for which $q_k h_k > q_j h_j$. If $g_j = 1$ (e.g., if species j is the highest-quality host in the community), each cowbird will attempt to parasitize each nest of species j she finds, assuming each cowbird is able to produce eggs at a rate sufficient to parasitize all nests of species j that she encounters.

For such a host species j,

$$t_j = T - \sum \left[s_l n_l (r - \gamma_l) \middle| l \in L \right],$$

where T is the proportion of total time that is spent searching for nests and L is the set of species l for which $h_l q_l / s_l > h_j q_j / s_j$. This is complicated by the possibilities that T and r may vary with host community composition (relative and absolute densities), cowbird density, food resources, etc. This equation for t_j can be used with Eq.

(5) to determine β_j. The resulting value for β_j can be substituted into Eq. (4), along with the value obtained for g_j from Eq. (7). This formulation expresses that a female cowbird should allocate time to searching for less favorable species only if she is first able to locate nests of all more favorable species.

These models that explicitly incorporate multiple host species exhibit several properties that may be important in understanding variation in natural levels of parasitism. First, level of parasitism may vary greatly among different host species at the same site as a function of variables such as host preference and abundance. In the case of a species numerous enough for some of its nests to avoid parasitism, the level of parasitism will decrease with increasing nest availability. Second, the level of parasitism of a given species may vary as a function of the relative densities and qualities (as hosts) of other species within the community. For instance, in the presence of a high density of preferred hosts, a less favorable host may remain largely unparasitized. Third, the specific model examined here predicts that at least one host species (the one with the highest search payoff) should be highly parasitized. If a female cowbird is not able to find all nests of the most favorable species, she should not invest time searching for nests of other species. If cowbirds can find all nests of the most favorable species, one or several less favorable species should be parasitized at intermediate levels. Other species may be parasitized at still lower levels as a result of random encounters.

This model is overly simplistic in that it does not consider within-species variation among individual hosts (e.g., in quality) and cowbirds (e.g., in preference and behavior). Existing data sets typically show patterns more complex than those predicted by the model, but it may be fruitful to examine these predictions in a simple system with few host species. It will also be valuable to consider host community composition when formulating models of parasitism that incorporate spatial patterns of cowbird behavior.

D. Functional Responses of Spatial Activity Patterns

Gates and Gysel (1978) suggested that the edge effects they observed resulted from functional and perhaps numerical responses of nest predators and cowbirds to elevated nest densities along ecotones. They attributed elevated levels of nest predation to increased "activity" of predators along edges, and they considered this a functional response to nest density. Many species of mammalian predators have home ranges that are large relative to the width of a sharp ecotone but may concentrate much of their activity along the edge. From a population-dynamic perspective, this may not represent a numerical response to nest density, but the effect may well be increased realized predator densities along the ecotone. I use the term "pseudo-numerical response" to refer to spatial and temporal gradients in local realized abundances of predators or cowbirds that result from variation in activity patterns in response to nest density gradients.

As with nest predation, Gates and Gysel (1978) attributed elevated levels of cowbird parasitism along edges to functional and perhaps numerical responses of cowbirds to nest density. Their description of a numerical response was "an influx of cowbirds from surrounding areas," which seems to imply immigration. It is not clear that immigration of cowbirds is any more relevant to edge effects than is immigration of nest predators. Cowbirds appear to have large but well-defined ranges, with feeding, breeding, and roosting areas that are distinct and often disjunct and distant from one another (Thompson, 1994; Rothstein *et al.*, 1986). If they concentrate their activity along edges because of elevated host densities, this is a pseudo-numerical response. Elevated densities of cowbirds along ecotones seem no more likely to result from true numerical responses than do elevated densities of nest predators. In any event, there is evidence that suggests that host abundance and cowbird abundance are related (Thompson *et al.*, 2000; Donovan, *et al.*, 1997; Evans and Gates, 1997; Donovan, 1994).

Donovan (1994) found that cowbird abundance (males and females summed) was positively correlated with host abundance among sites in forest fragments in central Missouri, but found no such relationship within the heavily forested Ozarks in southern Missouri (but see Donovan *et al.*, 1997). This is especially surprising given that she also found that correlations between cowbird abundance and all landscape variables examined were opposite in sign from correlations between host abundance and the same respective landscape variables. Cowbird abundance was negatively correlated with percent forest cover and positively correlated with perimeter-to-area ratio (within 1-10 km radii), whereas host abundance was positively correlated with percent forest cover and negatively correlated with perimeter-to-area ratio. It is probable that these landscape effects were largely influenced by differences between the central-Missouri forest fragments and the Ozarks. The correlation between host density and cowbird density, on the other hand, was significant only within the fragmented sites. It would be interesting to examine the relationship between host density and landscape structure within the fragments. If host density is higher in fragments with more edge, cowbirds may choose areas based on the extent of edge.

Donovan (1994) suggests two possible mechanisms to explain the observed relationship between host and cowbird abundance. Cowbirds may assess and respond to host abundance (pseudo-numerical or immigrative numerical response). Alternatively, cowbirds may experience higher breeding success in areas of higher host density and, through natal philopatry, increase their numbers in such areas (reproductive numerical response). There is, however, a third possible explanation: cowbirds may be attracted by structural cues to areas where host density is high (Evans and Gates, 1997). For instance, cowbirds may be attracted (either through immigration or through daily activity patterns) to field-forest edges. This behavior may be adaptive if host density is higher at such sites, even if cowbirds do not use host abundance as a direct cue. I refer to such mechanisms as "structure-directed responses" and will discuss them in Section E. In the current section, I focus on numerical and pseudo-numerical responses.

Regardless of whether correlations between nest abundance and cowbird/predator abundance are to be regarded as functional or numerical responses, these effects can be modeled by considering predator and cowbird densities to be functions of nest density. In order to do so, we must consider cowbird spacing behavior.

The extent to which female Brown-headed Cowbirds defend breeding territories is not clear, and there is evidence for geographic variation in their territorial behavior (reviewed in Rothstein *et al.*, 1986). Territory defense may not be advantageous in areas where the ratio of host abundance to cowbird abundance is very low, such as the Great Plains (Dufty, 1982; Elliot, 1980). The extent of territory defense by female cowbirds will influence the relationship between host density and cowbird density.

In an earlier contribution (Winslow, 1999), I used a power function to model pseudo-numerical or numerical responses of cowbird density to nest availability. I showed that level of parasitism could only increase with increasing nest availability if a numerical response worked in concert with a functional response of encounter rate (see Section B). I further argued that application of the concept of an ideal free distribution (Fretwell and Lucas, 1969) suggests that cowbirds would not be likely to respond numerically to changes in nest availability if parasitism is limited by encounter rate. This latter conclusion, however, was based on the questionable use of level of parasitism as an index of population-level cowbird reproductive success. Furthermore, it overlooks the fact that the ideal free distribution concept is inherently a numerical response model. Here I reject this approach in favor of an ideal free distribution model that employs rate of cowbird fledgling production as an index of population-level reproductive success.

If cowbirds are non-territorial, we might expect them to be dispersed according to an ideal free distribution with respect to nest availability within their breeding habitat. If so, we expect cowbird density would vary with nest availability in such a way that the fitness of individual cowbirds does not vary spatially (Fretwell and Lucas, 1969). If we consider the rate of cowbird fledgling production per female cowbird (F_c) as a measure of mean fitness, we can express this quantity as a function of P, C, and N:

$$F_c = E_c Q \exp(-\delta P / N), \tag{8}$$

where $E_c = P/C$ is the rate per female cowbird that cowbird eggs are laid in host nests, Q is the proportion of cowbird eggs laid in otherwise unparasitized host nests that fledge cowbirds, and $\delta > 0$ is the exponential decline in cowbird fledging success with increasing parasitism. This decline in fledging success is expected because the incidence of multiply parasitized nests will increase with increasing parasitism levels, contributing to intraspecific competition.

If cowbirds are freely distributed with regard to nest availability, cowbird density can thus be modeled as

$$C = \frac{N}{\delta E_c} \ln_e\left(Q \frac{E_c}{F_c}\right),$$

for positive δ over spatial gradients of nest availability (Figure 2.3a). If parasitism is limited by the rate of cowbird egg production ($E_c = \alpha$), cowbird density increases in direct proportion to N. If parasitism is limited by encounter rate ($E_c = \gamma N$), the response function is decelerating. If $\delta = 0$, there is no relationship between N and C ($C = CQE_c/F_c = C$) and the models of parasitism discussed previously (egg limitation or finding-rate limitation) will apply.

The ideal free distribution model assumes that female cowbirds are completely non-territorial. If cowbirds defend territories, we might expect them to follow an ideal dominance distribution (Fretwell and Lucas, 1969). If so,

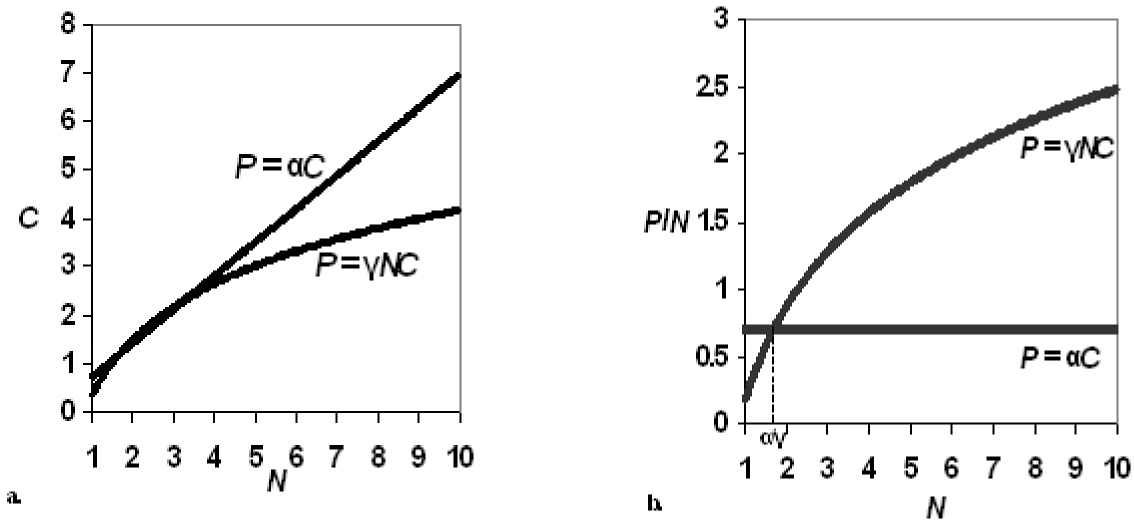


Figure 2.3: (a.) Ideal free distribution model of pseudo-numerical or numerical response of cowbird density (C) to nest availability (N), incorporating egg limitation ($P = \alpha C$) and encounter rate limitation ($P = \gamma NC$) parasitism functions. (b.) Level of parasitism as a function of nest availability when cowbirds follow an ideal free distribution with regard to nest availability. See Figure 2.1 for definitions of symbols. When $N < \alpha/\gamma$, parasitism will be limited by encounter rate ($P = \gamma NC$). When $N > \alpha/\gamma$, parasitism will be limited by cowbird egg production ($P = \alpha C$). This model predicts that level of parasitism will increase with increasing nest availability (over spatial gradients in N) at low values of nest availability. Where $N \geq \alpha/\gamma$, level of parasitism remains constant.

at high nest availabilities F_c would be higher and thus cowbird densities would be lower than predicted by an ideal free distribution model, as a result of exclusion of competitors by dominant individuals. The numerical (or pseudo-numerical) response function may be even further dampened because a population of host nests represents a number of different species that do not necessarily defend territories interspecifically, and thus cowbird densities may not be able to track spatial gradients in nest density at high levels of *N*.

Data presented by Donovan (1994) and Thompson *et al.* (2000) show fairly rectilinear relationships (although with much scatter) between host abundance and cowbird abundance, suggesting that female cowbird density is not limited by territoriality and that parasitism is limited by the rate of cowbird egg production. However, the census points sampled in these studies were dispersed over wide areas. The ideal free distribution approach may be more appropriate for the examination of cowbird densities over local gradients in nest availability.

Under the assumption of an ideal free distribution, F_c remains constant over spatial gradients of N. We can thus rearrange Equation 8 to solve for the level of parasitism:

$$P / N = \frac{\ln_e(QE_c / F_c)}{\delta}, \delta > 0.$$

Under the egg limitation model, $E_c = \alpha$ and thus

$$P / N = \frac{\ln_e(\alpha Q / F_c)}{\delta}.$$

Note that under the egg limitation model the level of parasitism remains constant with increasing *N* (Figure 2.3b), because E_c is not a function of *N* and cowbirds are distributed such that F_c remains constant over gradients of *N*. This differs from the prediction of the egg limitation model with numerical response presented previously (Winslow, 1999, Figure 3b), where *P/N* decreases with increasing nest availability. This latter situation may occur if dominant cowbirds exclude competitors from habitat where nest availability is high.

It is worth recalling that *P/N* is not necessarily equivalent to the level of parasitism as measured over an entire breeding season. Since *N* and *P* are likely to vary over the course of a season, model predictions will be dependent on the relationships of these variables with time. The index *P/N* can serve, however, as a measure of instantaneous level of parasitism and can be measured over short intervals during which *P* and *N* are constant. I now consider how this index varies with *N* when parasitism is limited by the rate at which cowbirds find nests.

Under the encounter-rate limitation model [Eq. (2)] with pseudo-numerical response,

$$P / N = \frac{\ln_e(\gamma NQ / F_c)}{\delta}.$$

Thus the level of parasitism increases logarithmically with increasing nest availability (Figure 2.3b). The level of parasitism can thus increase with increasing nest availability, if both functional and numerical (or pseudo-numerical) responses operate.

This theoretical framework suggests that the type of "functional" (pseudo-numerical) response of parasitism to host abundance envisioned by Gates and Gysel (1978) can occur only if cowbird parasitism is limited, during at least a portion of the breeding season, by the rate at which cowbirds encounter nests.

Models based on variation in nest density and functional and numerical responses will be more complex if they incorporate multiple host species that vary in relative abundance and in preference by cowbirds. The characteristics of such models may be helpful in understanding indirect interactions among host species. For example, Fretwell (1977) found that Dickcissels were more highly parasitized by cowbirds when breeding Red-winged Blackbirds were present than when red-wings were absent. In contrast, Clark and Robertson (1979) found that Yellow Warblers were less highly parasitized in the presence of breeding red-wings. More recently, Barber and Martin (1997) found that parasitism levels of Black-capped Vireos (*Vireo* *atricapillus*) and White-eyed Vireos (*V. griseus*) at Fort Hood, Texas, are positively correlated with the abundance of Northern Cardinals (*Cardinalis cardinalis*). Models of nest predation, when they incorporate multiple predator species that differ in prey preferences, will be even more complex. Another complicating factor is the direct effect of landscape features on cowbird and predator densities.

E. Structure-directed Responses

If nest densities are higher along ecotones, it may be adaptive for nest predators and brood parasites to direct their activities along such edges. That is, they may use structural aspects of vegetation as cues instead of responding directly to perceived nest abundance (Evans and Gates, 1997). O'Conner and Faaborg (1992) showed that abundance of cowbirds decreases with distance to edges, both exterior and interior, in large forest tracts in the Missouri Ozarks. A simple model incorporating this type of edge effect is

$$C=\frac{N}{\delta E_c}\ln_e\left(Q\frac{E_c}{F_c}\right)-\eta D^{\theta},\eta>0, \tag{9}$$

where D is distance to the edge and η and θ are constants. Partial correlation analysis can be used to calculate the effect of distance while accounting for the effect of nest availability, and vice-versa. This control is necessary, because nest availability will likely vary with distance to edge.

The relationship between nest availability and distance to edge may take an algebraic form similar to that for cowbird density and distance:

$$N = \iota - \kappa D^{\lambda}, \iota > 0, \tag{10}$$

where ι, κ, and λ are constants. If we combine this edge effect of nest density with the encounter-rate limitation model [Eq. (2)] and the edge effect of cowbird density described above [Eq. (8)], the level of parasitism will decrease with increasing distance as long as κ, λ, η, and θ are all positive.

If a structure-directed response is adaptive for cowbirds in that it allows cowbird abundance to track nest abundance, we should be able to describe the relationship without the distance term in Equation 9:

$$C = \frac{\iota - \kappa D^{\lambda}}{\delta E_c} \ln_e (Q \frac{E_c}{F_c}).$$

Under these conditions level of parasitism remains constant with change in distance to edge if cowbird density is not limited by territoriality (i.e. F_c does not vary over spatial gradients of N) and parasitism is limited by cowbird egg production (i.e. $E_c = \alpha$). If parasitism is limited by encounter rate (i.e. $E_c = \gamma N$) and cowbird density is not limited by territoriality, parasitism level will be elevated near edges. Alternatively, dominant cowbirds could monopolize habitat close to edges, depressing parasitism levels. If parasitism is limited by cowbird egg production, parasitism levels may even decline with increasing proximity to edge. It is therefore not clear that parasitism will always be higher near edges, even if cowbird densities are higher there.

One structural attribute of an ecotone that may attract cowbirds is the abundance of high-visibility perches within the trees and snags along the edge. These perches may be useful for nest-searching (Gates and Gysel, 1978) or courtship display (Mayfield, 1965), or both. Evans and Gates (1997) found a positive association between snag basal area and cowbird abundance in forest edge habitats in Maryland. Freeman and coworkers (1990) have suggested that the presence of trees in the nesting areas of Red-winged Blackbirds in Washington marshes increases the ability of

Brown-headed Cowbirds to lay eggs in appropriate nests (i.e., those in which host eggs are being laid). Also, Clotfelder (1998) found that parasitized nests of prairie-breeding Red-winged Blackbirds in Wisconsin were more likely to be located near trees than were unparasitized nests. However, Brittingham and Temple (1996) did not find that nests near snags were more likely to be parasitized, among forest-breeding birds in south-central Wisconsin.

Increased perch availability is an example of a factor that may elevate cowbird parasitism in the absence of increased host abundance. Other structural characteristics of edges may also influence cowbird abundance. Evans and Gates (1997) presented evidence that aspects of the vegetation structure at edges may influence abundance of both cowbirds and hosts. Both abundance of cowbirds and of hosts at forest edges in Maryland were positively associated with total volume of vegetation, although covariation of vegetation volume with other variables makes it difficult to interpret causation. Cowbird abundance also tended to be positively associated with snag basal area and foliage-height diversity. If structural aspects of vegetation at edges have important influences on cowbird densities, the structure-directed response model (Eq. 9) could be adapted to include these effects. Nest predators may also be influenced by structural attributes of edges.

Many species of nest predators may prey facultatively upon nests (Howlett and Stutchbury, 1996; Vickery *et al.*, 1992), and their distributions may thus not be significantly affected by spatial patterns of nest density (Fretwell, 1972). In such cases, what appear to be numerical responses to nest density at edges may in fact result from habitat selection. Predator species that prefer ecotonal or early-successional habitat may occur in greater numbers near some types of edges. In southern Illinois forests, for instance, Suarez and coworkers (1997) found higher levels of predation of Indigo Bunting (*Passerina cyanea*) nests along exterior (agricultural and old field) edges than interior edges (treefall gaps, streams, small timbercuts, and maintained wildlife openings). They suggested that this might result from increased use of edges or agricultural fields, or both, by raccoons (*Procyon lotor*), Blue Jays (*Cyanocitta cristata*), crows (*Corvus* spp.), and black rat snakes (*Elaphe obsoleta*).

These findings illustrate the importance of considering the specific mechanisms involved in observed patterns; edge effects associated with a certain type of ecotone may not be generalizable to other landscape contexts. Some predators, such as squirrels and chipmunks (Sciuridae), may even be more abundant within undisturbed forest than near edges (Hannon and Cotterill, 1998).

F. Use of Adjacent Habitat by Predators and Cowbirds

Edge effects of nest predation or brood parasitism may result from predators’ or brood parasites’ use of the adjoining habitat, rather than from attraction to the edge *per se*. For instance, cowbirds feed almost exclusively in short-grass or bare-ground habitats (Thompson, 1994; Rothstein *et al.*, 1986), and we might expect parasitism to be elevated in forest adjacent to pasture. This type of mechanism would not, however, explain elevated levels of parasitism near clearcut edges, because cowbirds do not feed in clearcuts.

Frazer (1992) found cowbird abundance to be higher within clearcuts in the Hoosier National Forest in Indiana than in surrounding forest, but did not find a consistent relationship between cowbird abundance and distance to edge within mature forest. Other workers have found higher numbers of cowbirds within clearcuts and openings than in adjacent forest (Winslow *et al.*, unpublished data; Annand and Thompson, 1997; Miles, 1995). Thus cowbirds, as well as some nest predators, may choose breeding areas based on the presence of successional habitat or other structural attributes (such as snags) that may be present in forest openings.

Pseudo-numerical or numerical responses to nest density may also result in high cowbird abundance within forest openings, independently of true edge effects. Host densities may be as high within a small island of early-successional habitat (e.g., a young clearcut) within continuous mature forest as they are along the edge between habitat types. Frazer (1992) measured avian abundance within clearcuts of varying age and within mature forest in south-central Indiana. She found the highest numbers of individuals and species within young (3-4 yr) clearcuts, with abundance and species richness declining with the age of cuts. Avian abundance in mature forest was lower than in these youngest cuts but greater than in older cuts.

If cowbirds or predators use adjoining habitat rather than the edge itself, patterns similar to those discussed for the structure-directed response (Section E) should occur. One difference, however, is that there should be no edge effect within the habitat that serves to attract the predators or the brood parasites. For instance, if cowbirds are attracted to clearcuts, parasitism within clearcuts should be uniformly high. If they are attracted to clearcut edges, however, parasitism within a clearcut should be highest near the forest edge and should decline toward the center of the clearcut.

G. Numerical Responses

Since nest density may be elevated near edges, nest predators and brood parasites may occur in higher numbers in these areas if their populations track nest density as a resource. Recent work, however, suggests that cowbird populations are regulated at spatial scales too large to explain edge effects (Thompson *et al.*, 2000; Donovan *et al.*, 1997; Robinson *et al.*, 1995; Donovan, 1994). Brown-headed Cowbird numbers appear to be determined primarily by distance from the center of their breeding range (the Great Plains) and secondarily by patterns of land use within distances of 3-10 km. If so, it seems unlikely that host breeding densities would have important effects on the local population dynamics of cowbirds or nest predators (but see Grzybowski and Pease, 1999).

Densities of cowbirds and nest predators may, on the other hand, affect the population dynamics of breeding birds. Nest predation may often have more important effects on prey populations than on predator populations (Fretwell, 1972). Also, brood parasitism by a generalist parasite (like the Brown-headed Cowbird) probably has more important effects on host populations than any given host population has on the parasite’s population dynamics (May and Robinson, 1985). If populations of nesting birds decline in response to high levels of nest predation (or parasitism), there might even be negative correlations between nest density and predator density (or cowbird density). Birds disperse readily, however, so populations may be maintained through immigration. For this reason, if predator or cowbird populations respond numerically, we may expect positive correlations between nest density and predator density (or cowbird density). May and Robinson (1985) modeled the effects of a generalist brood parasite on the population dynamics of a single host species, but did not extend the analysis to multiple host species or to effects of hosts on parasites.

If spatial variation in nest density and predator density are important in the population dynamics of both predators and prey, detailed models will be necessary in order to generate predictions regarding levels of nest predation in forest near internal edge. Fortunately, many nest predators may not rely on nests as an important food resource and so may not respond numerically to nest density (Howlett and Stutchbury, 1996; Vickery *et al.*, 1992). A possible exception is the rat snake; avian prey (eggs, young, and adults) comprises 20-50 % of the diet of this North American reptile (Ernst and Barbour, 1989).

H. Alterations in Vegetative Structure near Edges

Variation in vegetative structure near edges may affect the ability of nest predators and brood parasites to find nests. Norman and Robertson (1975) observed cowbirds using different search tactics in different habitats. Suarez *et al.* (1997) suggest that nests may be more visible along abrupt edges, but may remain well-hidden in gradual edges with thick undergrowth. The formulations developed herein for cowbird parasitism could be adapted to reflect this possibility by allowing β and γ to vary with distance to edge. For host species that nest close to the ground, the dense undergrowth near edges should increase nest concealment and thus decrease the probability of predation or parasitism (but see Howlett and Stutchbury, 1996). For subcanopy and canopy nesters, however, the open canopy that exists near an edge may cause predation or parasitism to increase. Thus alterations of vegetative structure near edges may affect the vulnerability of different species of nesting birds in various ways.

Martin (1992) briefly reviewed the evidence that nest concealment affects risk of predation. He concluded that increased concealment decreases predation risk, although some studies have not detected such an effect. Howlett and Stutchbury (1996) measured characteristics of Hooded Warbler

(*Wilsonia citrina*) nest sites and found no difference in concealment or any other measured characteristics between nests that were and were not preyed upon. In addition, their vegetation-removal manipulations at nest sites revealed no difference in predation of nests at manipulated and control sites.

These results are particularly relevant to modeling edge effects, because Hooded Warblers nest in dense cover within the shrub layer of forests. Since the shrub layer is often well-developed near edges, Hooded Warblers often nest near edges in managed forest landscapes (personal observation). If predators concentrate activity along edges and if increased concealment near edges fails to compensate, nest success of Hooded Warblers may be low in landscapes with extensive internal disturbance. Again, however, it is important to bear in mind that alterations of vegetation near edges will affect species with different nesting ecologies in different ways.

The two preceding paragraphs pertain to nest predation. Fewer studies have addressed effects of edge-associated vegetative alterations on brood parasitism. Brittingham and Temple (1996) compared the sites of parasitized and non-parasitized nests in Wisconsin forest and found that the former were characterized by more open subcanopy and canopy vegetation and denser ground cover. This finding is difficult to interpret because the sample included nests of 13 species with very different nesting ecologies. The one species for which the sample was adequate to examine separately was the Acadian Flycatcher (*Empidonax virescens*), a subcanopy nester. Acadian Flycatcher nests that were parasitized were characterized by subcanopy and canopy more open than that of non-parasitized nests, but parasitized and non-parasitized nests did not differ significantly in density of ground cover below them.

I. Edge Effects on Nest Predation

I have concentrated my discussion of the effects of edge on brood parasitism by the Brown-headed Cowbird, because that phenomenon is much simpler than the effects of edge on numbers and behavior of multiple predator species. Incorporating nest predation into the framework developed above is a challenging task, but parasitism may not be fully understandable without addressing edge effects on predation. Elevated predation will have the effect of increasing N by increasing the rate at which the owners of unsuccessful nests renest. Of course, it would not be adaptive for cowbirds to concentrate activity in areas where nests are more available because nest predation is high. It is reasonable to assume that cowbirds respond to the density of breeding adults, rather than to the density of nests *per se*.

Although it is easier in the field to estimate densities of breeding hosts than nests, this approach requires addressing the relationship between host densities and nest densities. Also, if the rate at which individual hosts initiate nests is influenced significantly by variables such as predation level and progress of season, these relationships will need to be taken into account to make predictions about parasitism levels (Pease and Grzybowski, 1995).

To develop mechanistic models of spatial patterns of nest predation it is helpful, if not necessary, to identify the relevant predators. Predator species may behave differently with regard to edges. Unfortunately, it is not always simple to determine what predators are important in nesting studies. Nest predators implicated in the studies reviewed by Paton (1994) included mammals (racoons; opossums, *Didelphis virginiana*; skunks, *Mephitis mephitis*; foxes, *Vulpes vulpes*; sciurids, etc), birds (notably corvids), and snakes. A wide variety of animals may prey upon nests, either facultatively or more habitually.

Evidence presented by Arcese and Smith (Arcese *et al.*, 1996; Smith and Arcese, 1994; Arcese *et al.*, 1992) suggests that Brown-headed Cowbirds may themselves be important predators of Song Sparrow nests on Mandarte Island, B.C. If so, and if the same is true of most areas where cowbirds are present, predation by cowbirds could be critical to understanding edge effects on avian productivity. However, the avian community on Mandarte is atypical, and it is not yet clear how well these results can be generalized. The population of Song Sparrows on Mandarte Island fluctuates greatly from year to year. There are almost no alternate hosts for cowbirds, and in most years only one or two female cowbirds breed on the island. Such a simple and well-studied system is a very important resource for investigating mechanisms of species interactions, but it is not necessarily straightforward to generalize to more complex situations.

Cowbirds often locate nests in forested habitats by watching the hosts during building (Norman and Robertson, 1975; Hann, 1941), which Arcese *et al.* (1996) suggest may be efficient in forests but not effective on Mandarte Island. On Mandarte it appears that cowbirds find nests by systematic searching, and Song Sparrows there begin to nest before the cowbirds start laying (Smith and Arcese, 1994). Thus many nests that cowbirds encounter are discovered too late to be parasitized. Arcese *et al.* argue that it is therefore adaptive to destroy such nests in order to stimulate renesting. Cowbird reproduction on Mandarte may well be limited by the rate at which nests become available [e.g. (Eq. 2)], whereas forested habitats often contain many alternative hosts with varying nesting phenologies. Therefore, cowbirds in forests may have ample nests to choose among and may not be compelled to destroy nests they are unable to parasitize.

AN APPROACH FOR TESTING THE MODELS

A. Interrelations among the Models and Hypothesis-testing

In order to understand how the formal models presented in this chapter relate to one another, it is helpful to examine the conditions under which they apply (Table 2.1). Some of the models are specific cases of more general models. For instance, Model 2 represents an instance of Model 4 where $\gamma = 0$. The conditions described for each model in Table I are in some cases more restrictive than necessary for the algebraic formulations to be valid. For instance, one condition listed for Model 4 is that $\beta > 0$. Model 3 is actually a special case of Model 4 that applies when $\beta = 0$. Thus the algebraic formulation of Model 4 is still valid when $\beta = 0$, but I have listed $\beta > 0$ as a condition because it must be met for the described qualitative predictions to be valid. The same is true in the other cases in which the conditions described in Table 2.1 are over-restrictive.

Predictions of the Models

Examination of the predictions of each model (Table 2.1) reveals that most of them yield qualitatively similar predictions for the relationship between nest availability and level of parasitism. For models without numerical or pseudo-numerical response, level of parasitism decreases or remains constant with increasing nest availability. Level of parasitism increases with increasing nest availability under Model 9. Structural response models may also exhibit increasing parasitism with increasing N (as illustrated by Model 10), depending on how cowbird density and nest availability vary with distance to edge and each other. Because the simpler models fail to yield this prediction, I suggest that elevated nest densities in proximity to edges can cause elevated levels of parasitism only if both functional and numerical (or pseudo-numerical) responses occur. It is important to bear this point in mind when interpreting the results of nesting studies.

The qualitative predictions described in Table 2.1 are not sufficient to test my suggestion that both functional and numerical responses are necessary for the existence of density-dependent edge effects of parasitism level, or to

Table 2.1: Statements and predictions for models of parasitism limitation.

Model	Limiting factor	Conditions under which model applies[a]	Algebraic description[a]	Qualitative predictions[b]
1	Egg-laying rate (null model)	$N \geq \alpha/\gamma + \beta/r - \beta/\gamma$, $\delta = 0$, $\eta = 0$	$P = \alpha C$	Parasitism level decreases with increasing nest availability
2	Search time	$\gamma = 0$, $N \geq \beta/r$, $\beta \leq \alpha$, $\delta = 0$, $\eta = 0$	$P = \beta C$	Parasitism level decreases with increasing nest availability
3	Encounter rate	$\beta = 0$, $0 < N \leq \alpha/\gamma$, $\delta = 0$, $\eta = 0$	$P = \gamma NC$	Parasitism level remains constant with changes in nest availability
4	Finding rate	$\beta/r \leq N \leq \alpha/\gamma + \beta/r - \beta/\gamma$, $\beta > 0$, $\delta = 0$, $\eta = 0$	$P = \beta C + \gamma(N - \beta/r)C$	Parasitism level decreases with increasing nest availability

5	Nest initiation	$0 < \beta = rN \le \alpha$, $\delta = 0$, $\eta = 0$	$P = rNC$	Parasitism level remains constant with changes in nest availability; all nests are parasitized
6	Finding rate (one host species)	$\beta_i/r \le n_i \le (\alpha/\gamma_i + \beta_i/r - \beta_i/\gamma)/g_ih_i$, $\beta_i > 0$, $\delta = 0$, $\eta = 0$	$p_i = \{\beta_i + \gamma_i(n_i - \beta_i/r)\}g_ih_iC$	Parasitism level for species *i* decreases with increasing nest availability
7	Finding rate (preferred host species)	$0 < \beta_i = rn_i \le \alpha$, $\delta = 0$, $\eta = 0$	$p_i = rn_ih_iC$	Parasitism level for species *i* remains constant with changes in nest availability; all nests of species *i* are parasitized
8	Egg-laying rate (with numerical response)	$N \ge \alpha/\gamma + \beta/r - \beta/\gamma$, $\delta > 0$, $\eta = 0$	$P = \dfrac{N\ln_e(\alpha Q/F_c)}{\delta}$	Parasitism level remains constant (if F_c is constant) or decreases with increasing nest availability

9	Encounter rate (with numerical response)	$\beta = 0$, $0 < N \leq \alpha/\gamma$, $\delta > 0$, $\eta = 0$, $dF_c/dN < \gamma Q$	$P = \frac{N\ln_e(\gamma NQ/F_c)}{\delta}$	Parasitism level increases with increasing nest density
10	Encounter rate (with structure-directed responses of cowbird density and host density)	$\beta = 0$, $0 < N \leq \alpha/\gamma$, $\delta > 0$, $dF_c/dN < \gamma Q$, $\iota > 0$, $\kappa > 0$, $\lambda > 0$, $\eta > 0$, $\theta > 0$	$P = \frac{N\ln_e(\gamma NQ/F_c)}{\delta} - \gamma N\eta D^{\theta}$, where $N = \iota - \kappa D^{\lambda}$	Parasitism level decreases with increasing distance

---

[a] See Appendix for meanings of symbols. The conditions stated are those for which the described qualitative predictions apply. In some cases these conditions are more restrictive than would be necessary for the algebraic descriptions to apply; see text.

[b] See Appendix for meanings of terms.

distinguish among the various models. Of course, each algebraic model describes quantitative predictions that are potentially testable if the variables and parameters can be estimated. For instance, Model 1 describes a hypothesized relationship among the rate (per unit area) at which cowbird eggs are laid in host nests, the rate of egg production per female cowbird, and the density of female cowbirds. If each of these variables can be measured, the validity of the model can be tested directly, as discussed in the following subsections.

Estimating Reproductive Parameters from Nest Data

Pease and Grzybowski (1995) developed techniques for estimating seasonal fecundity from nest data for a single host species, incorporating the effects of brood parasitism and nest predation. These techniques can be extended to estimate two of the variables, N and P, that appear in the models in Table 2.1.

I define nest availability (N) as the (temporal) rate per unit area at which nests are initiated. This is equal to $\sum n_i$, where n_i is the rate per unit area of nest initiation for each host species i within the community. Pease and Grzybowski (1995) introduced a similar parameter, $u(0,s)$, which is the proportion of breeding females in a monitored population of birds that are initiating a nest on day *s* of the breeding season. They explain how this parameter can be calculated from the temporal rates of nest predation and fledging and several other measurable parameters. If *u*(0,*s*) is multiplied by the density of breeding females of host species *i* (H_i), the rate per unit area at which new nests are initiated is

$$n_i(s) = H_i u(0,\ s).$$

The *s* in parentheses on each side of the equation indicates that these parameters can be calculated for each day in the season (or for longer intervals) in order to account for within-season heterogeneity.

I define $P = \sum p_i$ as the temporal rate per unit area at which cowbird eggs are laid in host nests, for all host species $i \in I$. This is similar to the concept of ρ introduced by Pease and Grzybowski (1995), which describes the rate (per day) at which parasitism events occur in a sample of monitored female breeding hosts. From this can be calculated

$$p_i(s) = \int_{t_e}^{t_i} H_i \left[\rho_u u(t,s) + \rho_p p(t,s) \right] dt,$$

where (as defined by Pease and Grzybowski, 1995) t_e is the time in the nest cycle at which nests become available for parasitism (near the onset of laying), t_i is the time in the nest cycle at which nests become unsusceptible to parasitism (near the time of clutch completion), ρ_u is the rate at which unparasitized nests are parasitized, $u(t,s)$ is the proportion of host females that are at day t in the nesting cycle and are unparasitized on that day, ρ_p is the rate at which previously parasitized nests are parasitized again, and $p(t,s)$ is the proportion of host females that are at day t in the nesting cycle and are parasitized on that day.

Pease and Grzybowski (1995) describe techniques for estimating these parameters. Their approach provides a great deal of flexibility to incorporate variation in model parameters, but it can also be used to formulate simple models in which parameters are assumed to be constant. One valuable attribute of their approach is that it permits incorporation of seasonal variation in nest availability, parasitism rate, and predation rate. Thus it is possible to calculate P and N at different times in the breeding season, which greatly facilitates the testing of the models of edge effects presented in this chapter.

Estimating Parameters using Regression

Some of the other parameters of the models in Table 2.1 (such as β and γ) may not be directly measurable, but they may be estimated using regression analyses. In order to explore how to do so, I examine some of the simpler models and assume that the density of female cowbirds does not vary with nest availability or with variables related to nest availability. If *P* is regressed on *N* with a simple linear model (Model 4), γ can be estimated from the slope of the regression and an estimate of cowbird density (*C*). β can be estimated using the y-intercept, the estimates for γ and *C*, and an estimate of female cowbird home range size (*r*). To test the hypothesis that *P* increases with *N*, the *F* distribution can be used to contrast the variance explained by this regression with that explained by a null hypothesis of $\gamma = 0$. Both Models 1 and 2 describe such a null hypothesis, so the level of significance indicated by this *F*-test can be regarded as an expression of the degree of confidence that a functional response of parasitism to nest availability has occurred.

In practice, unfortunately, it will be generally very difficult to estimate *P* directly; more likely *P* will be obtained from estimates of *P/N* and *N*. In such cases it might be more appropriate to divide all the terms in Model 4 [Eq. (3)] by *N* to obtain

$$\frac{P}{N} = \gamma C + \frac{\beta C(r - \gamma)}{rN}.$$

With the model in this form, a nonlinear regression of *P/N* on *N* will estimate parameters. This model statement ($y = A + B/x$) can be tested against a null hypothesis of 0 y-intercept ($y = B/x$). For instance, using Model 1 [Eq. (1)] as a null hypothesis, dividing all the terms by *N* will produce

$$\frac{P}{N} = \frac{\alpha C}{N}.$$

An *F*-test of a regression model with a constant (y-intercept) versus a model with no constant would thus make it possible to determine whether *P* increases significantly with increasing nest availability. If the null hypothesis is rejected, it may be concluded that parasitism is limited by a cowbird nest-finding rate that increases with increasing nest availability.

If the null hypothesis is not rejected, the parameter estimate for αC can be divided by an estimate of cowbird density to obtain an estimate of α. If this value is similar to published values of the cowbird's egg-laying rate (which during peak cowbird breeding has been consistently measured as 0.7-0.8 eggs per day among wild females; Fleischer *et al.*, 1987; Rothstein, *et al.*, 1986), it may be concluded that parasitism is limited by the cowbird’s rate of egg-laying. If the estimated value of α is significantly lower than 0.7 eggs per day (again tested using an *F*-test), it might be concluded that parasitism is limited by a constant (not dependent on nest availability) rate at which cowbirds find host nests (β).

B. Testing Alternative Mechanisms of Edge Effects

It will often be difficult to make field measurements sufficient to test these models quantitatively. Also, the similarity in qualitative predictions of the models makes it difficult to discriminate among them without quantitative tests. For these reasons it is necessary to consider how these algebraic models work together to describe mechanisms of edge effects.

Table 2.2 lists the various mechanisms proposed herein that may explain edge effects of cowbird parasitism. Understanding each mechanism generally requires incorporating two or more of the algebraic models. Table 2.2 presents assumptions that ideally should be verified before testing each mechanism, as well as qualitative predictions of the proposed mechanisms that follow from the specific formal models. In this section I describe how each mechanism may serve to cause edge effects and discuss how the assumptions and predictions may be tested.

Functional Response to Nest Density

According to the framework developed herein, a simple functional response to nest density should not by itself cause an increase in level of parasitism with increasing nest density. For this reason, if nest density increases in proximity to edge, this mechanism (a functional response to nest density) is not sufficient to explain elevated parasitism levels near edges. In Section A, I described how one might determine whether a functional response has occurred. Such a determination does not in itself help to explain elevated parasitism near an edge, however, if nest density is higher there.

It may be possible, nevertheless, to test whether my formulation of a functional response is itself valid. If the formulation is valid and if cowbird density does not vary with nest availability, the level of parasitism should not increase with increasing nest density. If cowbird density is found to remain constant over a gradient of host nest density, level of parasitism can be measured to test the formulation. If there is a positive relationship between nest density and parasitism level, this would suggest that my formulation of a functional response of encounter rate is flawed. Because host community composition is likely to change with changing nest density,

Table 2.2: Predictions of alternative mechanisms for edge effects of parasitism.

Mechanism[a]	Models involved[bc]	Testable assumptions of mechanism[c]	Qualitative predictions of mechanism
Functional response to nest density	3 or 4	C does not vary with N or with variables related to N.	Parasitism level decreases or remains constant with increasing N.
Variation in avian community composition	6 and 7	Parasitism level increases with increasing host quality and/or decreases with increasing level of aggression by hosts.	Parasitism level of given host species varies with avian community composition and densities of alternate hosts. Variation in parasitism level is not continuous, but distributed among 3 categories: highest quality host species highly parasitized, one host species parasitized at intermediate levels, other host species largely unparasitized.

Pseudo-numerical response	8 and 9	*C* increases with increasing *N*, independently of other variables (such as *D*) that may be related to *C* and *N*.	At low values of *N*, parasitism level increases with increasing *N*. At higher values of *N*, parasitism level remains constant or increases with increasing *N*.
Structure-directed response	10	*C* increases with increasing *D*, independently of other variables (such as *N*) that may be related to *C* and *D*.	Parasitism level decreases with increasing *D* in focal and adjacent habitats, independently of other variables (such as *N*) that may be related to *C* and *D*.
Response to adjacent habitat	10 in focal habitat; 8 and 9 in adjacent habitat	*C* increases with increasing *D* (independently of other variables) within focal habitat but not within adjacent habitat.	Parasitism level decreases with increasing *D* in focal but not in adjacent habitats, independently of other variables (such as *N*) that may be related to *C* and *D*.

Numerical response	8 and 9	C increases with increasing N, independently of other variables (such as D) that may be related to C and N.	At low values of N, parasitism level increases with increasing N. At higher values of N, parasitism level remains constant or increases with increasing N.
Alterations in vegetative structure	4 with dependence of β and γ on D (see text)	Vegetative structure varies with distance to edge. Parasitism level varies with structural characteristics at nest sites.	Variation in parasitism level with distance to edge is explained by variation in measured nest site characteristics. Parasitism level does not vary with D independently of nest site characteristics.

---

[a] See text for explanations of mechanisms.

[b] See Table 2.1 for model descriptions.

[c] See Appendix for definitions of terms and symbols.

it is also important to examine parasitism levels within individual host species. Variation in parasitism among hosts would confound the relationship between total nest density and parasitism level.

Variation in Avian Community Composition

Variation in avian community composition may be the basis for an apparent edge effect of parasitism or nest predation. For instance, if a certain species that nests in abundance near an edge is also a preferred cowbird host, parasitism level as measured over the entire avian community may be elevated near the edge. This measure may not indicate a true edge effect of parasitism if samples close to the edge are biased heavily toward the preferred host species (Bielefeldt and Rosenfield, 1997). For this reason it is necessary to test for edge effects within each host species.

Even a measured edge effect within a given species may result from changes in avian community composition as a function of distance to the edge. For example, if a preferred host species tends to nest at some distance from an edge, parasitism level for alternate hosts may decrease with distance to edge. The reason this may occur is that cowbirds searching for nests away from the edge will be more inclined to lay in nests of the preferred species. This is reflected by the dependence of g_j and t_j on the densities and characteristics of high-quality alternate hosts present in the community (see **Mechanisms of Edge Effects**, Section C). Alternatively, a pseudo-numerical or numerical response may occur and parasitism of the alternate host may be higher where the preferred species nests (Barber and Martin, 1997; Fretwell, 1977). In any case, if level of parasitism for a given host species varies with abundances of alternate hosts, this supports the notion that indirect interactions among host species are important. However, such an observed pattern does not insure that the specific model formulations presented in this chapter are valid.

If host species interactions are important, models that do not consider variation among hosts may in many cases be inadequate. Unfortunately, the multiple-species approach as presented here may also be overly simplistic. This is indicated by what appear to be unrealistic predictions: (1) almost all parasitized species are parasitized at high levels, (2) there is one host species (or, generously, several similar host species) parasitized at intermediate levels, and (3) other species are parasitized erratically or not at all (see **Mechanisms of Edge Effects**, Section C). Published studies typically show more continuous variation in parasitism than expected under these predictions (e.g., Winslow *et al.*, 2000).

This formulation for parasitism of multiple host species yields uncomplicated predictions (enumerated above) partly because it does not take into account many complicating factors, such as variation in the behavior of individual cowbirds and of individuals within host species, variation in nesting phenology among hosts, and interactions with the other mechanisms discussed in this paper. Two very important assumptions upon which this formulation depends are (1) that cowbirds prefer some host species to others and (2) that such host-choice decisions by cowbirds are adaptive. This second assumption can be tested using data from nesting studies, by determining whether level of parasitism is positively correlated with measures of host quality (such as cowbird fledglings produced per cowbird egg laid). Cowbird nest-selection decisions do not appear to be always adaptive, in any case, given that the birds sometimes lay in nests of rejector species (Rothstein, 1976).

Pseudo-numerical Response

Increased availability of nests near edges can lead to elevated levels of parasitism if a functional response of encounter rate is coupled with a numerical (or pseudo-numerical) response of increased cowbird density (Model 9, Fig. 2.3). The reason is that the swamping effect of the distribution of cowbird eggs among a greater number of nests is counteracted by both an increase in encounter rate per cowbird and an increase in cowbird numbers. Neither the functional response (Models 3 and 4) nor the pseudo-numerical response (Model 8) alone yields the prediction that level of parasitism rises with increasing nest density. Note that the model presented of encounter-rate limitation with pseudo-numerical response (Model 9) is based on the Model 3 functional response, as opposed to Model 4, and thus does not contain β. If $\beta > 0$ is included, nest availability and level of parasitism will still be positively related.

To determine if this mechanism is occurring in a natural system, the first step is to establish that there is a pseudo-numerical response. Although it might not be easy to obtain accurate estimates of cowbird density and nest availability, a positive correlation between cowbird abundance and host abundance derived from avian censuses would provide a strong suggestion of either numerical or pseudo-numerical responses (over space) to increased nest density.

Researchers should take care, however, to consider other variables that might affect measures of abundance of both cowbirds and hosts. For instance, if numerical response is considered a mechanism to explain edge effects, the reason is that both cowbird density and nest density are thought to be elevated near edges. Therefore it is necessary to consider simultaneously the effects of edge and host density on cowbird density. This can be accomplished using partial correlation or regression analysis (Section C).

If cowbird density and nest availability are related directly (independently of other variables), an attempt can be made to determine whether a functional response occurs in conjunction with the numerical response. If so, the models presented here predict that level of parasitism will increase with nest availability at low values of N and not vary over higher values of N. The formulation presented earlier (Winslow, 1999) predicted that parasitism would peak at intermediate levels of nest availability when both functional and numerical responses operate. Both patterns result from the limiting factor of cowbird egg production at high levels of nest availability (Compare Model 8 in this chapter with Model 8 in Table II of Winslow, 1999.). Figure 2.3 illustrates the increasing function of a numerical response with encounter-rate limitation (Model 9), overlain by the constant numerical response with egg limitation (Model 8). From this it appears that level of parasitism peaks at intermediate to high levels of nest availability.

If cowbird abundance increases in an accelerating function with host density, this might be taken as evidence that cowbirds follow an ideal free distribution with parasitism limited by the generalized finding rate model (Model 4), i.e.

$$C = \frac{N \ln_e\left[Q\left\{\beta + \gamma\left(N - \beta/r\right)\right\} / F_c \right]}{\delta\left\{\beta + \gamma\left(N - \beta/r\right)\right\}}.$$

However, this would be a situation where it would clearly be advantageous for dominant cowbirds to exclude competitors. For this reason it seems unlikely that cowbirds would be freely distributed if the parasitism function contains both density-dependent and density-independent components.

Structure-directed Response

The structure-directed response mechanism is based on elevated density of cowbirds near edge habitat, as is the pseudo-numerical response mechanism. The former mechanism differs from the latter, however, in that cowbirds are assumed to be attracted to the edge itself, rather than to elevated nest availabilities near the edge. In concert with a functional response of encounter rate, a structure-directed response may cause elevated levels of parasitism near an edge. Whether this occurs will depend, however, on how exactly cowbird density and nest availability vary with distance to edge (i.e., on the values of η, ι, κ, and λ) and how cowbirds are distributed spatially with regard to nest availability.

The structure-directed response model presented in Table 2.1 (Model 10) was obtained by combining a functional response of encounter rate [Eq. (2)], a structure-directed response of cowbird density to edge [Eq. (9)], and a relationship of decreased nest density with distance to edge [Eq. (10)]. The level of parasitism under this model will decrease with increasing distance to edge as long as η, θ, ι, κ, and λ are positive and as long as F_c does not vary with N at a rate that exceeds γQ.

Notice that Eq. (9) (and thus Model 10) also contains a term for a numerical/pseudo-numerical response of cowbird density to nest availability. This illustrates that numerical and structure-directed responses should be considered together, as discussed above under *Pseudo-numerical response*. The actual form of the relationship among these variables could be different than that presented in Table 2.1; for instance, there could be terms for interactions among distance and nest availability. Again, partial correlation or regression analysis can be used to separate the effects of these variables.

Response to Adjacent Habitat

The mechanism of a structure-directed response to adjacent habitat is similar to that to an edge, except that cowbirds or nest predators are attracted to the adjacent habitat rather than to the edge itself. For example, cowbirds may be attracted to clearcuts because of the views afforded by perches either along the edge or by snags within the clearcuts. In either case, cowbirds within mature forest will be more numerous near a clearcut.

The critical prediction to distinguish these models (of response to the habitat adjoining the edge as opposed to response to the edge itself) is that within the successional habitat cowbird density should decrease with increasing distance from the edge only in the case of an edge-directed response. If cowbirds respond to the disturbed habitat rather than to the edge, their densities should not vary within that habitat, or they might even increase toward the center of the disturbance.

In practice, however, it might be difficult to detect variation in densities of cowbirds within disturbances such as the relatively small clearcuts of eastern forests. Behavioral studies or experiments manipulating the presence of snags (Winslow, unpublished data) may help to determine the precise mechanisms involved.

Numerical Response

The models presented in this chapter do not permit a pseudo-numerical response and a numerical response to be distinguished (Table 2.2). A true numerical response would occur if cowbird populations actually increase through enhanced reproduction or immigration in areas of high nest availability. Radiotelemetry or demographic studies of marked individuals, or both, might be necessary to determine whether a true numerical response occurs.

Alterations in Vegetative Structure

Alterations in vegetative structure near edges may affect the ability of cowbirds and nest predators to locate nests. For many species of breeding birds, denser understory and increased ground cover that are usual near edges might keep nests well-concealed. This would serve to elevate nest success in forest near edges, contrary to typical concepts of edge effects. For birds that nest in the canopy or subcanopy, however, more open canopies near edges may reduce nest concealment and therefore success (Brittingham and Temple, 1996).

Although I have not presented a formal model to describe the effects of varying nest cover on parasitism level, the finding-rate models (in concert with a structure-directed response model) could be modified to represent such a mechanism. This could be accomplished by allowing the search-rate parameters (β and γ) to vary with distance to edge (D).

The first step in investigating whether this type of mechanism can cause edge effects would be to test the assumptions that nest-site characteristics (1) vary with distance to edge and (2) can affect levels of nest predation and cowbird parasitism. Many studies have measured nest-site characteristics to determine whether they affect predation or parasitism, or both, with varying results (e.g., Hoover and Brittingham, 1998; Burhans, 1997; Cresswell, 1997; Brittingham and Temple, 1996; Howlett and Stutchbury, 1996; Norment, 1993; other studies reviewed in Martin, 1992).

If nest site characteristics are found to meet the assumptions enumerated in the preceding paragraph, a structure-directed response model (such as Model 10, but perhaps incorporating Model 4 rather than Model 3 to describe finding rate) could be modified such that β and γ vary with D. This model could be quite complex, especially if interspecific differences in nesting ecology are taken into account. It is likely that testing such a model would require an approach such as path analysis.

C. Path Analysis

The path diagram shown in Figure 2.4 summarizes the important variables discussed in this chapter and their proposed relationships. Path analysis can be used to

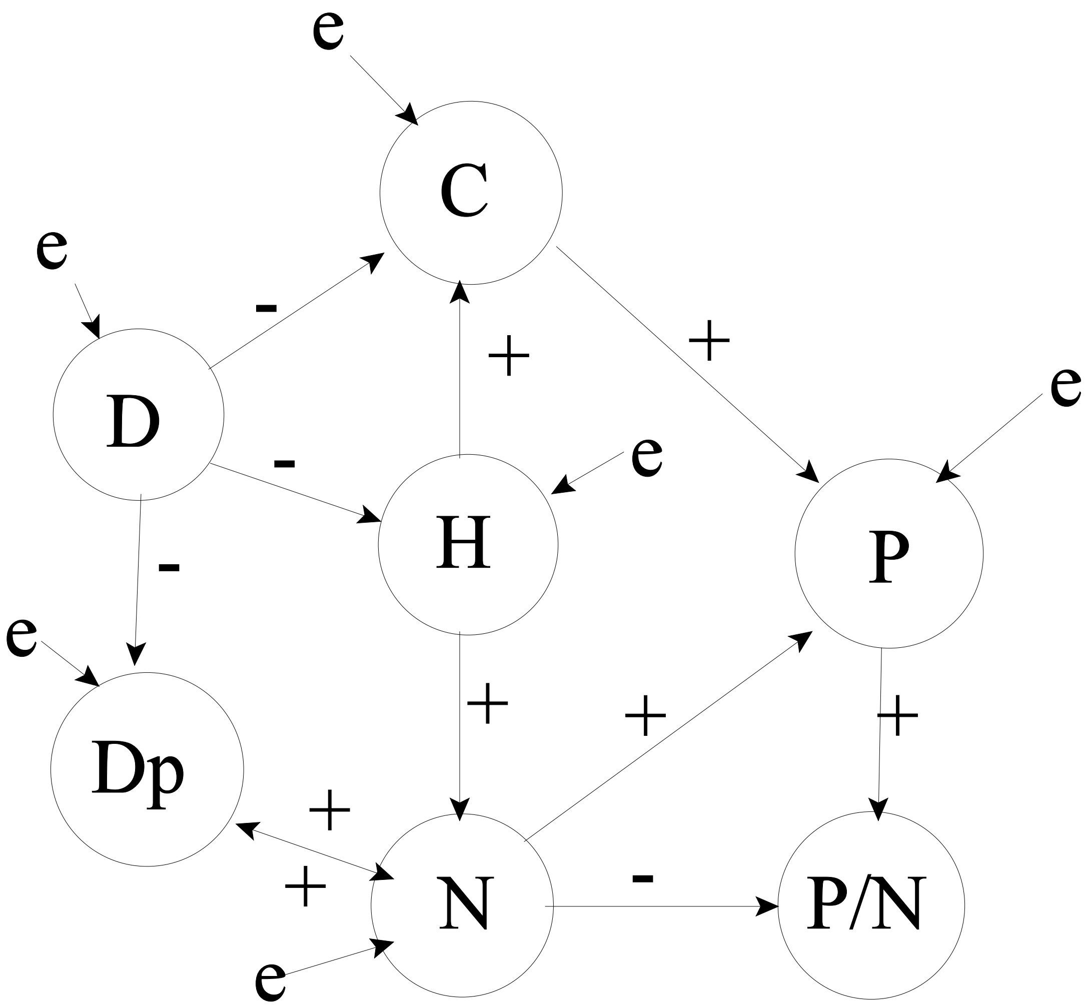


Figure 2.4: Path diagram showing relationships among variables that may affect level of parasitism. *C* = cowbird density, *H* = host density, *N* = rate at which host nests are initiated per unit area, *D* = distance to edge, *Dp* = level of depredation, *P* = rate at which cowbird eggs are laid in host nests per unit area, *P*/*N* = level of parasitism, *e* = error terms. Arrows show directions of proposed effects; + and - indicate whether the effects are expected to be positive or negative, respectively.

determine how well each of the proposed effects explains the variation observed in the model parameters. It is not always easy, however, to measure each variable for every species involved.

Fortunately, it may be possible to compartmentalize the path into smaller units that can be more readily evaluated. For instance, the triangle formed in the diagram by *D*, *C*, and *H* (host density) is assumed not to be influenced by any of the other variables (as indicated by the absence of arrows pointing from other variables toward *D*, *C*, and *H*). We should thus be able to use partial correlation analysis to determine the independent effects on cowbird density of host density and distance to edge, without being concerned with the other variables. Similarly, partial correlations can be employed to determine the independent effects of host density and distance to edge on the level of nest depredation (*Dp*)(here the intermediate variable *N* drops out as part of the relationship between *Dp* and *H*). Although it may be difficult to estimate *P* in many cases, the full path can be analyzed if the other variables can be measured, because *N* and *P* completely determine the level of parasitism, *P/N* (indicated by the absence of an error term influencing this variable, Sokal and Rohlf, 1995). It should therefore be possible to evaluate all these relationships, provided differences among host species are unimportant.

The path is more complex if multiple host species are considered. The strengths of relationships among *C*, *H*, and *D* can be evaluated for individual host species and for all host species pooled. If some of the relationships are seen to be unimportant, the path may collapse into a more tractable model. Host species of high quality should influence cowbird densities more strongly than less preferred species. If so, it will be possible to examine the influence of the densities of preferred hosts on the levels of parasitism of nests of other species.

It may nevertheless be important to consider the presence of low-quality hosts. In many North American avian communities there are species that consistently eject cowbird eggs, which makes it difficult to measure the level of parasitism accurately. The presence of ejector species may reduce parasitism pressure on other species in the community, by acting as "sinks" for cowbird eggs (Grzybowski and Pease, 1999). Variation in the abundance of ejector species may be a factor that would complicate attempts to apply the models presented in this chapter.

Other complicating factors include seasonal variation in *P*, *N*, and *Dp*. For example, predation levels in some systems are high early in the season but much lower late in the season (e.g., personal observation; Wilson and Cooper, 1998; Nolan, 1978; Gottfried and Thompson, 1978). It is possible to measure these variables over small time intervals (e.g., weeks), but the sample sizes on which such values would be based may be unacceptably low. It may be necessary to concentrate analysis on the peak of the breeding season, when P, N, and Dp should remain relatively constant.

CONCLUSIONS: IMPLICATIONS FOR RESEARCH AND CONSERVATION

The theoretical explorations in this chapter constitute only a first step toward understanding the mechanisms underlying edge effects on avian productivity. I hope that researchers will use this effort as a springboard to develop these ideas more fully, to construct alternative models, and to investigate assumptions and predictions of these and other models through empirical studies in the field. We cannot assume that phenomena observed in one ecological system will apply to other systems, which may vary in community composition, habitat structure, etc. In order to make informed decisions about resource and land use, it is imperative that we understand the causes of edge effects. It remains as important as it ever was for land management agencies to conduct studies to monitor avian productivity in varying habitats and landscape contexts. Academic researchers, however, should focus research on questions addressing the mechanisms that control breeding success.

Countless species of organisms are threatened by fragmentation in our world today. As human encroachment continues and phenomena such as global warming and stratospheric ozone depletion alter environmental conditions in ecosystems everywhere, we are certain to lose much of the biological wealth that is our heritage. Migrant birds have advantages over many taxa, as they can disperse over large distances and colonize available habitat with relative ease. Understanding the factors that influence avian population dynamics is nevertheless of vital importance, because long-distance migrants represent biological connections between the ecological communities of the world. But for this very reason, determining what factors limit and otherwise influence avian populations is an especially difficult problem. Careful, thoughtful, theoretically-based, empirical studies in all components of these species’ ranges are required. Until such understanding is obtained, the precautionary principle demands that we minimize habitat fragmentation of all types as much as is possible.