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THE INTERACTION OF NEST PREDATION AND BROOD PARASITISM: FACTORS AND CONSEQUENCES OF RE-NESTING IN SONGBIRDS

By

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ABSTRACT

THE INTERACTION OF NEST PREDATION AND BROOD PARASITISM: FACTORS AND CONSEQUENCES OF RE-NESTING IN SONGBIRDS

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Most research of the breeding biology of songbirds fails to explicitly account for the influence of re-nesting after nest predation. Not only can re-nesting ameliorate the effects of nest predation but it can also lead to an unusual effect where nest predation enhances seasonal fecundity (relative to when nest predation is absent) if brood parasitism is frequent. This is because when nest predation occurs on parasitized nests, it acts as a rejection mechanism for cowbird acceptors. A dynamic quantitative model is introduced that can simulate the nesting cycle of many species of single-brooding songbirds, and is used to explore this interaction between nest predation and brood parasitism. Simulation results confirm that a significant interaction between nest predation and brood parasitism can exist such that at high parasitism frequencies, intermediate levels of nest predation led to small positive changes in seasonal fecundity. This increase is enhanced when the cost of parasitism is severe, there is greater nest predation on parasitized nests, and the risk of parasitism and predation declines through the breeding season. In general, nest predation ranging from zero to as high as 60% does not reduce seasonal fecundity when moderate to high parasitism (>60%) exists in the breeding population.

A review of the literature and field results of a monitored population of Yellow Warbler confirm that all the special conditions required to observe this benefit to nest predation could occur in a natural population. However, it remains unclear if all necessary conditions would occur collectively in a single population. Moreover, repeated nest predation on some individual bird's nests decreases the ability of re-nests to recover losses from nest predation. Field observations and field experimentation comparing nest success of actual nests with artificial nests suggests that some individuals, namely younger parents, occupy lower quality territories that increase the chance of nest failure. This leads to an overall greater failure rate for re-nests compared to initial nest attempts, and eliminates the potential for a benefit to nest predation regardless of other conditions. Since many populations show age-specific variation in nest success, it is concluded that a beneficial effect to nest predation is unlikely to occur often in natural populations. Regardless, the complex interaction of nest predation and brood parasitism with various other factors such as age and habitat quality has significant management consequences. Proper management strategies will depend greatly on an accurate assessment of these interactions that will unquestionably vary inter- and intra-specifically both spatially and temporally. Further use of advanced simulation modeling will greatly improve the ability of managers and researchers to efficiently conserve avian populations, which in many cases have been declining for several decades. To improve these models, future field research will have to focus more on seasonal fecundity instead of nesting success by explicitly accounting for the re-nest attempts of individual birds.

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TABLE OF CONTENTS

LIST OF TABLES

Table Page

LIST OF FIGURES

CHAPTER 1- INTRODUCTION

Brood parasitism by the Brown-headed Cowbird (*Molothrus ater*) and predation on eggs and nestlings are widely implicated in the decline of several Neo-tropical migrant bird species (Terborgh 1989, Askins et al. 1990, Martin 1992a, Robinson et al. 1995a). Habitat fragmentation has been linked to increased frequencies of both mortality factors (Gates and Gysel 1978, Brittingham and Temple 1983, Wilcove 1985, Robinson 1992). Because of extensive fragmentation of the North American forest landscape, moderate or high frequencies of nest predation and brood parasitism exist together in many songbird populations. Most field studies that have attempted to evaluate the impact of these two mortalities have used nest success as an index to overall reproductive success (Pease and Grzybowski 1995). Nest success does not account for replacement nests (re-nests) that typically follow a nest failure. Nor do measures of nest success explicitly identify how nest predation and brood parasitism interact. Only very recently have we begun to examine how these two causes of nest mortality interact to influence seasonal fecundity in songbirds (Pease and Grzybowski 1995, Schmidt and Whelan 1999). The way in which songbirds respond to these nest mortalities can be quite different and can lead to interesting interactive effects. The aim of this dissertation is to discuss the interaction of nest predation and brood parasitism and the effect of this interaction on seasonal fecundity for Neo-tropical migrant songbirds that typically fledge one brood in a season.

Brood parasitism- Interspecific brood parasitism is when one species of bird, the parasite, lays its eggs in the nest of another species, the host, who then raises the parasite's young, often at the expense of its own young. There are at least 85 known obligate brood parasites in birds (May and Robinson 1985). Most brood parasites, such as those belonging to the family Cuculidae (Cuculiformes), are host specific, specializing on a single host or small subset of species. However, several members of the family Icteridae (Passeriformes) known as cowbirds will parasitize multiple hosts, of which the Brown-headed cowbird is the champion.

The Brown-headed Cowbird is the principle brood parasite of small terrestrial birds in North America. It is unusual among brood parasites in that it is known to parasitize a large number of bird species. Some estimates are as high as 216 host species (Robinson et al. 1995b). In general, brood parasitism by cowbirds has a three-fold negative impact on the fecundity of the host (Rothstein 1990). First, female cowbirds commonly remove a host egg when laying an egg. Second, cowbird eggs are often larger than the host's eggs and may hatch sooner thereby disrupting proper incubation of the remaining eggs. This may lead to an increase in hatching failure in host clutches. Finally, the cowbird hatchling has a voracious appetite and will often out-compete other nestlings for food provided by parents. Many host nestlings starve to death in parasitized nests. Unlike the cuckoos of Europe and Africa, cowbirds nestlings rarely eject host eggs and young from nests (Robinson et al. 1995a).

Variation in the response and performance of the host does exist among bird populations. Birds which have historically shared overlapping ranges with the Brown-headed Cowbird have evolved adaptive responses to brood parasitism. These include ejection of the cowbird egg, nest abandonment followed by a re-nest attempt, or building a new nest over the parasitized nest (Robinson et al. 1995a; Rothstein 1990). However, during the last two centuries the Brown-headed Cowbird has undergone a rapid range expansion (Mayfield 1965). This has led to many new populations of songbirds becoming exposed to brood parasitism. Most of these songbird populations have not evolved an adaptive response to brood parasitism (Brittingham and Temple 1983, Robinson et al. 1995a). Host species are categorized as either a rejector or acceptor depending on how individuals respond to the presence of a cowbird egg in their clutch. The majority of North American species are categorized as acceptors (Rothstein 1975). There is also considerable variation in performance when parasitized among acceptor species. Some species are capable of raising a cowbird nestling with minimal losses to their brood (Wolf 1987, Eckerle and Breitwisch 1997) while others suffer severe reductions in fledgling success (Goldwasser et al. 1980, Walkinshaw 1983). Many small Neo-tropical migrant songbirds experience elevated host young mortality from brood parasitism. This is because the cowbird nestling is often larger than the parents and occupies the majority of space in the nest. Consequently, many small hosts cannot provide enough food for the aggressive cowbird nestling and their own brood, which is often concealed by the cowbird nestling (for examples see Nolan 1978, Rothstein 1990, Robinson et. al. 1995a).

Many Neo-tropical migrants must also deal with another problem. Because they must allocate time to migrate long distances, most only have time to successfully raise a single brood in a short breeding season. Birds that can raise only a single brood will not lay an additional clutch after they have fledged young. If a cowbird successfully fledges from the nest, the host parents typically behave as if they have produced a successful clutch, even if none of their own young survived. Clearly, the potential cost in terms of seasonal fecundity for parasitized individuals can be great for Neo-tropical migrant songbirds. It is for this reason that cowbird parasitism has been implicated in the decline of many migrant songbirds (Brittingham and Temple 1983). It is members of this group of birds that are the subject of the remainder of this dissertation.

The frequency at which nests become parasitized varies greatly with host species, region, habitat, and landscape. For most host species, brood parasitism occurs in less than 50% of nest attempts. However, brood parasitism rates have been regularly observed to be quite high. For example, bird populations nesting in southern Illinois have consistently experienced parasitism rates as high as 80% of all active nests (Robinson et. al. 1995b). Instances of even higher parasitism frequencies can be found in the literature, and in fragmented forests, it is not uncommon to find frequencies of brood parasitism greater than 50% for many preferred hosts (Robinson et al. 1995a). With natural frequencies this high, there is a potential for large reductions in seasonal productivity in some populations. The ultimate cost of brood parasitism on a population will depend on the life history of the species, how frequent brood parasitism occurs in the population, and as we will see, the interaction with nest predation.

Nest predation- In contrast to brood parasitism, nest predation typically results in loss of the entire brood. Nest predation is the removal or destruction of the contents of a nest by another organism. Nearly every breeding bird population experiences some degree of nest predation. In North America many organisms are known to depredate the nests of birds including many mammals such as raccoons, skunks and several rodents, reptiles such as snakes, and other birds, especially corvids (Corvidae: crows and jays). When a nest becomes depredated many birds will quickly respond by constructing a replacement nest and laying another clutch. This is the case even for those birds that will only raise a single brood. In addition, if this re-nest is also depredated some birds may attempt another clutch and so on. The significance of this is that birds are able to recover most of the loss in fecundity from nest predation.

The total reproductive cost to nest predation will depend on how often a host will re-nest after failure. The potential to re-nest varies among populations, though field observations are surprisingly few in the literature (Martin and Li 1992). Nolan (1978) observed one female Prairie Warbler (*Dendroica discolor*) attempt eight replacement nests in a single season. Yet, in another study of Tree Swallows (*Tachycineta bicolor*), fewer than 50% attempted a single replacement nest, and of those that attempted replacements, only 12% made a third attempt (Rooneem and Robertson 1997). The probability that a bird will re-nest depends on a number of factors including the length of time available in the breeding season and the availability of resources to accommodate additional egg production. Nolan (1978) observed that the percentage of first nesting attempts that were replaced was constant and high through June (average of 89%) but rapidly declined to zero by mid-July; only one female attempted a new nest after July 1. This result suggests that there are trade-off's between producing a successful brood and other needs, such as preparing for the fall migration, molting, or even adult survival. A short-term benefit in fecundity by re-nesting may impose a higher cost in an individual's lifetime fecundity by increasing adult mortality (Linden and Moller 1989). It is also plausible that survival of young from later nests is lower, making it less advantageous to attempt additional nests.

There is usually a reduction in clutch size from one nest attempt to the next

(Ricklefs 1973, Nolan 1978, Rooneem and Robertson 1997). Yellow Warblers (*Dendroica petechia*) breeding in Michigan lay about one less egg per nest attempt. The magnitude of this clutch reduction is likely to vary between species and region. The size of the brood at fledging is also likely to be smaller by the same amount. The greater the proportionate reduction in brood size the greater the cost of nest predation. If we ignore any potential long-term costs to re-nesting such as lower fledgling survival of young from re-nests or lower adults survival, then the reduction in clutch size is the only immediate cost to nest predation in terms of seasonal fecundity for a single-brooding songbird.

The Interaction- This re-nest response can have important consequences when considering how nest predation and brood parasitism interact to influence seasonal fecundity. In most North American songbird populations, brood parasitism and nest predation can occur in the same nesting event. The typical events that can occur during a breeding season are summarized in Figure 1-1. If a bird's nest is parasitized, the bird can either care for the clutch, which could result in raising fewer young than normal, or terminate this nest attempt and start a new clutch. As Figure 1-1 depicts, nest predation is a plausible means of escaping brood parasitism for those songbirds that have not evolved a rejection mechanism. If re-nesting following nest predation fledges more young on average than would have fledged from the parasitized nest had it not been depredated then nest predation can be interpreted as enhancing fecundity for the host. It is important to recognize that this is only a relative benefit and is contingent upon the failed nest being parasitized and having a low potential for fledging many host young. Simply stated, nest

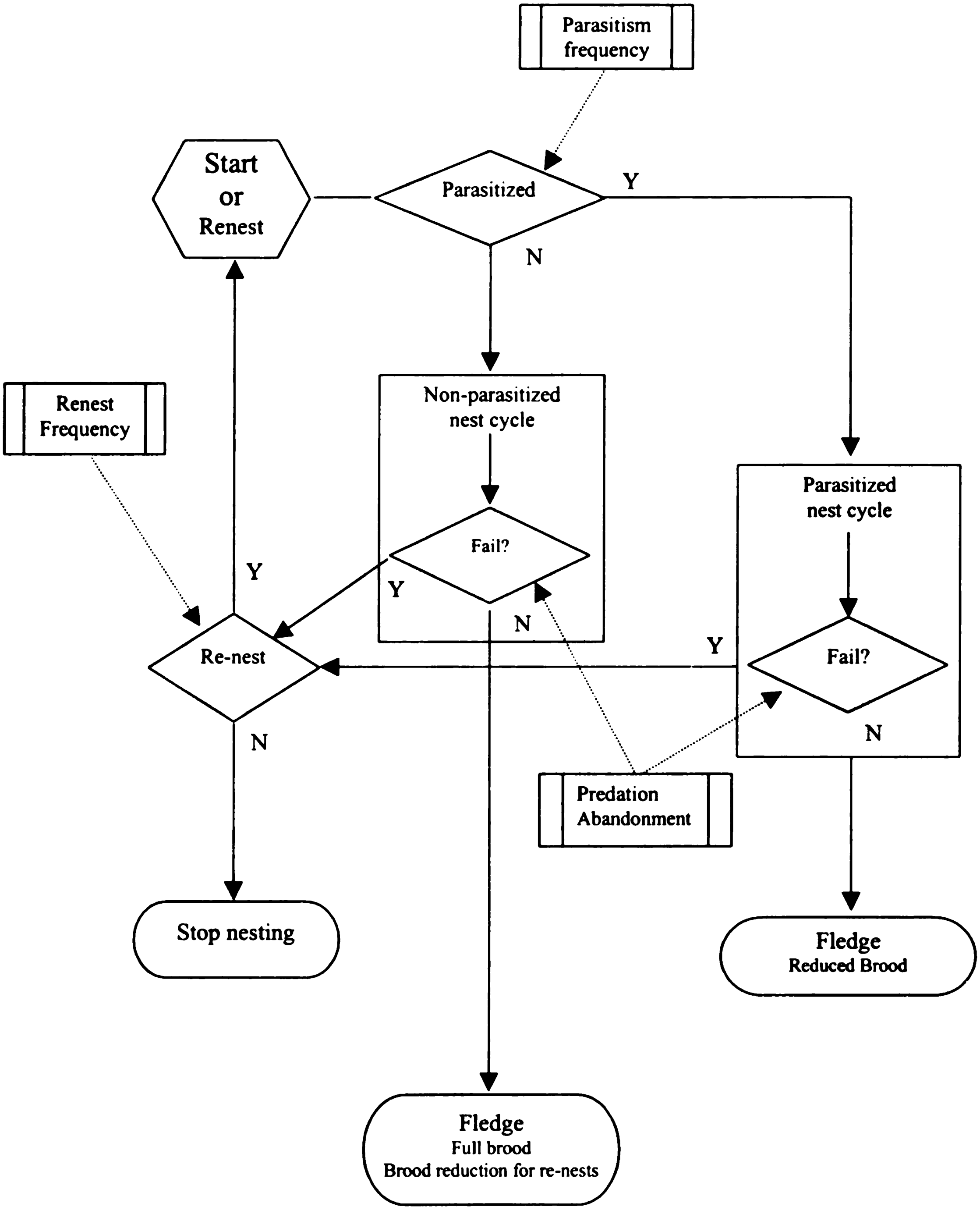


Figure. 1-1. The nest of a single-brooding songbird can follow many pathways depending on several internal and external factors as described here.

predation, in this case, is the lesser of two evils. I use the term benefit to describe the result for lack of a better term.

When a bird is unlikely to fledge any host young when parasitized, it is obvious that nest predation can improve their chance of successfully fledging young by means of re-nesting. It is much less obvious if nest predation can have this result in an entire population, since non-parasitized nests will also be depredated and re-nests can be parasitized or depredated. Two conditions are necessary for a benefit to nest predation to be possible in a songbird population. First there must be a significant level of brood parasitism since only these nests stand to gain from nest predation. In addition, re-nests must fledge more young on average than parasitized nests.

Even if these conditions are met, whether an actual benefit to nest predation is likely to occur greatly depends on the success of re-nest attempts. A re-nest is also susceptible to nest predation and parasitism. If repeated nest predation occurs, the bird could run out of time and energy to re-nest and fail to raise any young. There are several plausible means by which this may occur. In some cases the frequency of nest predation may simply increase later in the season (Beaver 1975), resulting in greater nest predation on re-nests. Sonerund and Fjeld (1987) found evidence that some avian nest predators may memorize the locations of previously discovered nests and repeatedly return to the same area, leaving re-nests more susceptible to nest predation. It is also possible for re-nests to be less successful relative to the average original nest attempt simply because those birds that re-nests are inherently less capable of rearing a successful nest.

However, there are also reasons to expect lower nest predation for re-nests. There is evidence to suggest that songbirds improve nesting success with experience (Saether

1990). Therefore, it is reasonable to expect that with each failed attempt birds gain experience to improve their chance of success in a subsequent nest attempt. Some also suggest that nest predation is density-dependent (Martin 1993b). Since some nests will succeed, the number of active re-nests is likely to be lower than the original number of nests. This temporal change in nest density should correspond to lower nest predation for re-nests if is density-dependency exists. While support varies between studies, nest concealment is believed to be an important characteristic of a successful nest. All else being equal, re-nests should be more concealed since vegetation in most habitats continues to grow during the season. For example, I commonly observed exposed small shrubs become completely concealed by fast growing tall grasses.

Re-nests that are initiated while cowbirds are still actively laying eggs remain at risk to brood parasitism. Most Brown-headed Cowbirds have an egg-laying season of approximately 10 weeks with most eggs laid in May and early June; very few cowbirds continuing to lay eggs into July (Nolan 1978, Wolf 1987, Brown 1994, Robinson et al. 1995a and references therein). However, for many songbirds nearly all nesting occurs during this same period. Therefore, when the frequency of brood parasitism is high the risk of re-nests becoming parasitized is also high. However, it is still possible for the risk to brood parasitism to decline. Egg-laying by cowbirds has been shown in many studies to peak early in the breeding season (early June) followed by a subsequent drop in frequency as the season progresses. For example, Hofslund (1957) found that most parasitism was concentrated in earlier nests of the Common Yellowthroat (*Geothlypis trichas*) and most re-nest attempts were free of cowbird eggs. If this trend is common we can expect that re-nests should experience lower brood parasitism rates.

Differences in nest predation frequency between non-parasitized and parasitized nests are also important to the outcome of a predation-parasitism interaction on a songbird population. There will be a greater relative cost to nest predation regardless of the success of re-nests, if nest predation is more likely to occur on non-parasitized nests than parasitized nests. Likely reasons for this include temporal or spatial differences in the risk to nest predation and brood parasitism, or nest predation by cowbirds. For example, while both nest predation and brood parasitism are widely known to increase in frequency in fragmented landscapes in eastern North America, the same is not true in the west. Tewksbury et al. (1998) have shown that western avian communities in fragmented habitat have greater rates of parasitism, but nest predation occurs more often in un-fragmented habitat. This suggests that some western species have lower nest predation on parasitized nests relative to non-parasitized nests.

At a smaller scale, increased predation on non-parasitized nests may be the direct result of cowbird behavior. Arcese et al. (1996) have hypothesized that adult cowbirds will depredate non-parasitized nests that have completed egg-laying in order to be able to parasitized the re-nest attempt. Also, Robinson (1992) found that nests placed on or near the ground had lower brood parasitism frequencies, while Ricklefs (1973) suggests that ground nests have the highest risk to predation. Thus, cowbirds may select host nests that are more likely to avoid nest predation (Tewksbury, pers comm.). If these patterns are real, nest predation is likely to occur more often for non-parasitized nests. However, considerable disagreement exists in whether such trends are common. Several studies have shown that lower nests are actually more often parasitized (Newman 1970, Smith 1981, DellaSalla 1985, Briskie et al. 1990). And while direct evidence for Arcese et al.'s hypothesis exists (Elliott 1999), no supporting evidence has been found beyond the unique conditions of their study area, which has few natural nest predators.

The relative frequency of nest predation on non-parasitized and parasitized nests is likely to depend on the predator community. Cowbirds are known to most often locate nests by monitoring adult movements (Norman and Robertson 1975). On the other hand, a diverse community of predators is likely to locate nests through a variety of means including adult activity, nest exposure, systematic searching, or opportunity (luck). Nest predators may use sight, smell, or sound to locate nests. If the predator community consists largely of diurnal nest predators that locate nests in a similar manner to cowbirds, then nest predation might occur more frequently on parasitized nests. This is because the same factors that made it possible for a cowbird to locate a nest are likely to make it easier for a predator to discover the nest. For example, Martin (1992b) suggests that the number of visits an adult makes to a nest can increase the risk to nest predation. This behavior can also increase the risk to brood parasitism (Norman and Robertson 1975). Furthermore, many songbirds must make more visits to a nest when feeding a cowbird nestling. Subsequently, nest predation may be expected to be higher on parasitized nests. Moreover, cowbird nestlings tend to beg loudly, and could conceivably increase the potential for predators to locate the nest (Dearborn 1999).

How nest predation and brood parasitism ultimately affect seasonal fecundity will depend on a large number of factors. Many of these deal with the success of subsequent nest attempts. Few studies have explicitly accounted for re-nests and factors influencing their success. Consequently, many of the factors that may influence re-nest success and the resulting interaction between nest predation and brood parasitism are largely unstudied. Recent modeling work has begun to explore this interaction and suggests that a benefit to nest predation is plausible (Pease and Grzybowski 1995, Schmidt and Whelan 1999). However, these papers did not explicitly investigate the potential benefit to nest predation from this interaction.

The objective of this dissertation is to begin to explore these issues using fieldwork and simulation modeling to understand how re-nests can influence seasonal fecundity and what influences the success of these re-nests. I will first discuss results from a nesting study of the Yellow Warbler focusing on the role of re-nesting and factors affecting the success rate of these nests (Chapters 2 and 3). I will then introduce a simulation model designed to predict seasonal fecundity for any single-brooding songbird under a variety of conditions (Chapter 4). This chapter will also discuss modeling results specific to the relative benefit to nest predation, and contributions of certain parameters to seasonal fecundity. Finally, in Chapter 5, I will examine one mechanism observed in the field that may prevent a benefit to nest predation from occurring in real populations, increased failure of re-nests.

CHAPTER 2- FIELD METHODS

A nest monitoring study was performed to explore how nest predation and brood parasitism interact in a natural population. This empirical study focused on the role of re-nests and factors affecting nesting success that may contribute to how nest predation and brood parasitism interact. This would improve our understanding of whether such interactions are likely to occur in real populations. Another goal of this aspect of the study was to collect data to evaluate the performance of the simulation model described in Chapter 4. This chapter describes details of the field study sites, the focal species, and methodology used to monitor and analyze data.

Field sites- Four field sites in south-central Michigan were used in this study. Two sites are within the Rose Lake Wildlife Research Area located at the southern end of Shiawassee and Clinton counties, approximately 19 km northeast of Lansing (Figure 2-1). Two other sites are located in the Dansville State Game Area in central Ingham County approximately 4 km south of Dansville (Figure 2-2). The Michigan Department of Natural Resources (DNR) manages both land areas. The DNR granted access to all sites for purposes of this study. Field sites range in size from approximately 6-12 hectares. Sites were selected according to accessibility, similarities in habitat and vegetation structure, and abundance of breeding birds as determined through observations made in early May 1997. Site boundaries in most instances are clearly defined close-canopy woodlands except that a small creek bounds one side of a site at Rose Lake.

Site 1 in Rose Lake is located along Stoll road 3 km west of Upton Rd (42° 48' 00" N and 84° 21' 50" W). This site, subsequently referred to as R-S, was monitored in

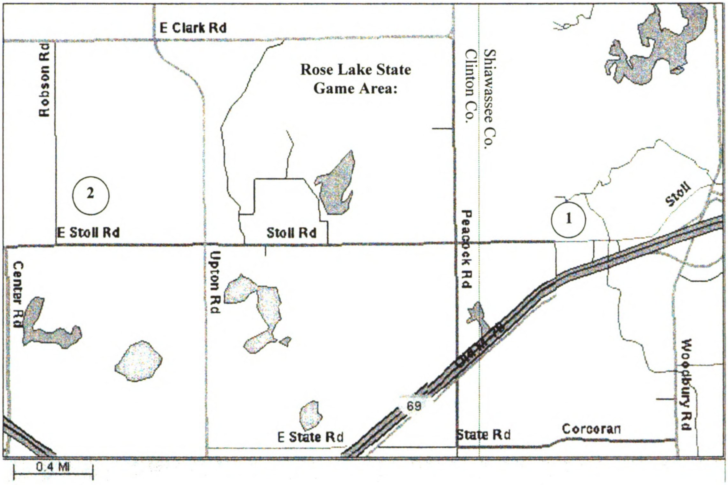


Figure 2-1. Map of lower Clinton and Shiawassee Counties in Michigan showing the locations of the two Rose Lake State Game Area field sites. Circled numbers indicate the locations of the sites. 1) Site 1: R-S, and 2) Site 2: R-R.

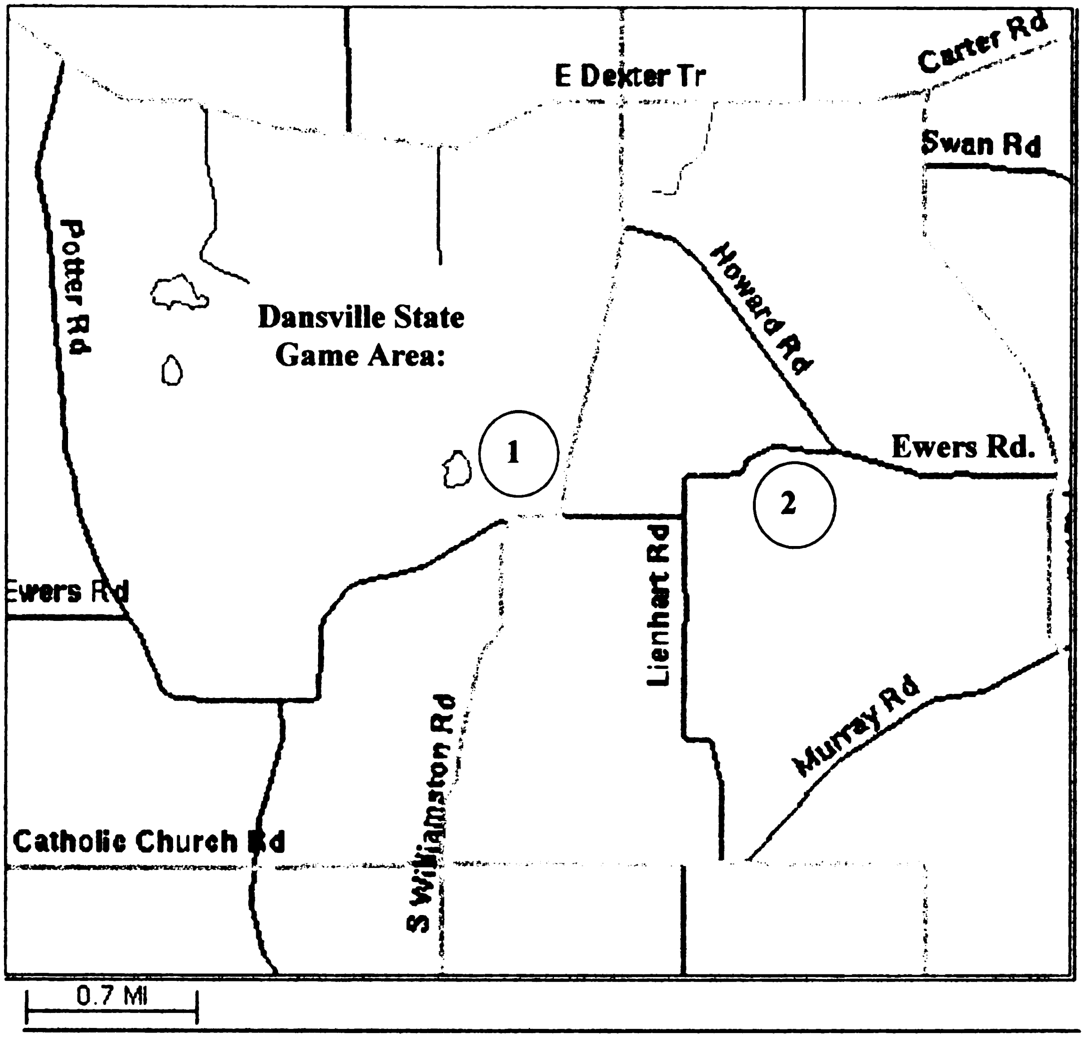


Figure 2-2. Map of central Ingham County in Michigan showing the locations of the two Dansville State Game Area field sites. Circled numbers indicate the locations of the sites. 1) Site 1: D-W, and 2) Site 2: D-E.

1997 and 1998. Site R-S was not monitored in 1999 and 2000 due to poor breeding densities of warblers and insufficient field assistants. Site 2 in Rose Lake, referenced as R-R, is located on the east side of Robson road, 0.5 km north of Stoll road (42° 48' 10" N and 84° 24' 35" W). This site was monitored in 1998 through 2000. Site 1 in Dansville is located at the northwest corner of the intersection of Williamston and Ewers roads (42° 30' 45" N and 84° 18' 00" W). This site referenced as D-W was monitored 1997 through 2000. The second site in Dansville is located on the south side of Ewers road 300 meters west of Howard road (42° 30' 45" N and 84° 16' 50" W). This site will be referred to as D-E and was monitored 1998 through 2000.

All field sites consist of similar wetland habitat characterized by a mosaic of shrubs and open marsh. Common shrubs on all sites include meadowsweet (*Spiraea latifolia*), red-osier dogwood (*Cornus stolonifera*), gray dogwood (*Cornus drummondi*) several species of willow (*Salix spp.*), and rose (*Rosa spp.*). These shrubs are typically organized as dense patches of varying size surrounded by patches of mixed sedges (*Juncus spp.*), grasses and occasionally cattails (*Typha spp.*). Trees are generally sporadic and include American Elm (*Ulmus americana*), Black Willow (*Salix nigra*), Silver Maple (*Acer saccharinum*), Red Maple (*Acer rubrum*), Box Elder (*Acer negundo*), Cottonwood (*Populus deltoides*), and Tamarack (*Larix luricina*). With the exception of site R-S, these sites had very dense populations of the focal species, Yellow Warbler, ranging from 2-3 breeding pairs per hectare. Other common breeding birds included Common Yellowthroat (*Geothlypis trichas)*, Swamp Sparrow (*Melospiza georgiana*), Song Sparrow (*Melospiza melodia*), and Red-winged Blackbird (*Agelaius phoeniceus*).

Focal Species- The primary objective of the field study was to monitor nesting activity of a songbird population in order to assess the consequences of re-nesting behavior on seasonal fecundity. To be able to evaluate the interactive impact of nest predation and brood parasitism this study population had to meet some basic conditions. The most important of these conditions is that the population must be a common cowbird host that is subject to significant losses to fecundity when parasitized. Two species nest in sufficient densities on the field sites and met these conditions, the Yellow Warbler (YWAR) and Common Yellowthroat (COYE). Both are members of the family Parulidae. Common Yellowthroat nests proved extremely challenging to locate since they tend to be placed in dense grass or sedge and adults were very secretive in approaching and leaving their nests. Despite considerable effort trying to locate their nests, only a handful was monitored each year. Alternatively, Yellow Warbler nests were readily located, thus nearly all the data discussed in this thesis concerns this species.

Yellow Warblers prefer shrubby wetlands but will nest in a variety of habitats (Brewer et al. 1991). While small declines in total population numbers have been observed in some regions, YWAR remain abundant throughout most of North America and are especially increasing in abundance in southern Michigan (Table 2-1). They are generally considered to be a leading cowbird host (Ehrlich et al. 1988). YWAR are known to occasionally recognize and reject nests that have been parasitized, by building a replacement nest directly over the parasitized nest (Burgham and Picman 1989). However, they tend only to reject nests that are parasitized early in the egg-laying stage and when there is sufficient time to re-nest. Burgham and Picman (1989) discovered that parasitism still accounted for 41% of all egg losses in their study population despite the rejection behavior. Therefore, this species was deemed a suitable candidate for observing the interaction between nest predation and brood parasitism.

Table 2-1. Breeding Bird Survey abundance trends for Yellow Warbler and Common Yellowthroat from 1966 to 1998 (Sauer et al. 2000). Trends were estimated using the route-regression method (Geissler and Sauer 1990).

Species	Region	Mean count	Trend	Variance	P-value
YWAR	Michigan	6.05	2.89	1.15	0.008
YWAR	Continental	4.33	0.68	0.0319	0.0053
COYE	Michigan	12.11	1.19	0.339	0.0446
COYE	Continental	7.72	-0.31	0.0204	0.0292

YWAR consistently return to lower Michigan during the last week of April (pers. obs, Brewer et al. 1991). Upon arrival, males quickly establish territories. Females arrive a few days after males, and select mates. Males aggressively defend their territory boundaries from con-specifics. However, different species will regularly occupy overlapping boundaries and do not exhibit territorial aggression toward each other. Skirmishes between con-specifics are commonly observed along territory boundaries. Observers used these skirmishes to delineate the boundaries of territories (Kendeigh 1944). Territory size, while not directly measured in this study, was estimated to range from approximately 500 to 1000 m^2. Adults remain on these territories until all nesting is complete, and do not change territories between nest attempts. YWAR are monogamous with pairs remaining together for the entire breeding season (Ehrlich et al. 1988, Brewer et al. 1991).

Depending on the local weather conditions courtship can last from a few days to two weeks. During an unusually cool spring in 1997, most YWAR did not begin nesting until the third week of May despite arriving near May 1. During mild springs in 1999 and 2000, YWAR nest construction was observed in the first week of May. Females construct nests from mostly plant matter including fine grasses, old milkweed stem fibers, and cotton-like plant fibers. In these sites, YWAR place nests in small shrubs, usually about one meter high (99.5 ± 2.72 cm, mean ± se, n = 257). Meadowsweet was the preferred nest plant though rose and dogwood were frequently used. Typical clutch size is 5 eggs, though clutch sizes of 4 are not uncommon (Ehrlich et al. 1988). Only one YWAR laid a clutch larger than 5 eggs (6 eggs). Females incubate the eggs, but both parents feed the young. Incubation typically lasts 11 days (Ehrlich et al. 1988). Hatching is synchronous and young typically fledge in 9 days (Ehrlich et al. 1988).

Upon fledging, the parents will continue to care for the fledglings for at least one week and remain on or near the original territory. Since fledging was rarely directly observed, this behavior was used in most cases to confirm that a nest had indeed fledged. YWAR do not attempt a second brood after fledging young, however, those whose nests failed, re-nested. While nearly all individuals attempted re-nests in May and early June, the frequency of re-nest attempts began to decline quickly during the third week of June (Figure 2-3). Most individuals would attempt nests up to 3 times in a season if time permitted. Rarely, four nest attempts were made (n = 3).

Nest monitoring- Nest searching and monitoring techniques follow the guidelines offered by Martin and Geuple (1993). These guidelines call for careful observations of adult activity to locate active nest sites. To be sure we located all nesting YWAR, we systematically searched each study site locating all active territories mainly by observing singing males. Generally, territories saturated each site with the exception of a few large grassy areas void of suitable nesting substrate for YWAR. Nests were most often located through carefully observing the female until her nest was located. Female YWAR regularly visit the nest site during nest construction. Consequently, most nests were located during this stage.

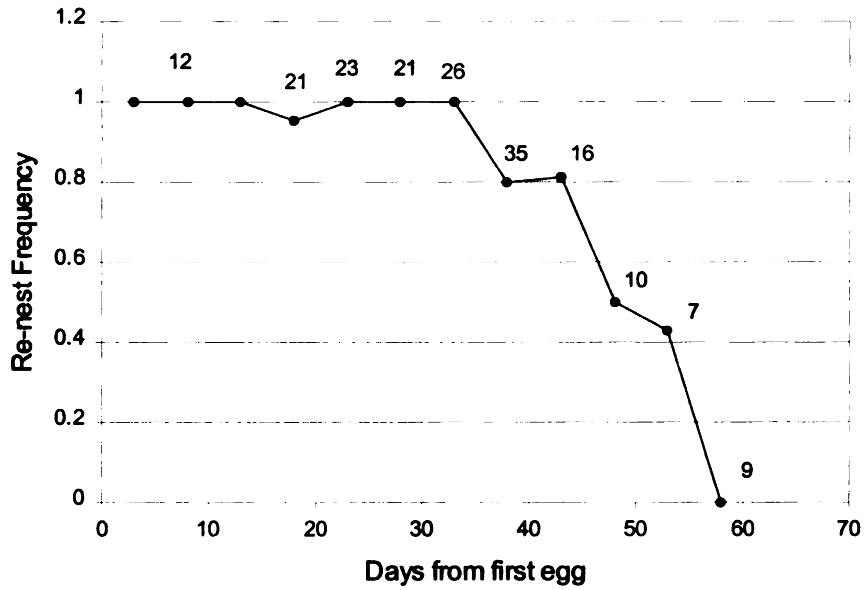


Figure 2-3. The frequency at which replacement nests are initiated following nest failure is very high in the first month of nesting, but declines rapidly in the second month (mid-June). Numbers represent the total number of nests that could potentially re-nest in an interval.

Upon locating a nest, a flag was tied to nearby vegetation. Marking the location of nests with flags placed near the nest has been shown to increase predation (Picozzi 1975). To minimize this, flags were placed more than 5 meters from the nest and were most commonly 8-10 meters away. The location of the nest was recorded on a nest card. Recorded information included, approximate nest location on the site, a compass bearing from the flag, estimated distance from the flag to nest (m), nest plant species, estimated nest height (cm), and a written description or drawing of the nest location from the flag.

Monitoring active nests may potentially influence nest success through observer disturbance (Gotmark 1992). The following efforts were made to minimize any biases caused by observer disturbances at the nest. In order to prevent abandonment, nests were generally not approached during construction unless adult behavior suggested that the nest was complete and egg-laying had begun. When the nest was complete, the nest contents were checked every 2-4 days by using a mirror attached to a 2-meter pole. This prevented any trampling of vegetation directly to the nest. In certain situations direct observations of the nest contents were made when the mirror could not provide a clear view of nest contents. After a complete clutch was laid the nest contents were not checked again until the estimated hatch-date, unless adult behavior suggested that the nest had been depredated. The nest contents were checked once more 2-3 days prior to fledging to confirm the number of young. The number of young fledged was assumed to equal the number of young present during this last check. Occasionally, the exact number of young could not be counted during the last check. In these cases, the total number fledged was assumed to equal the total number of hatched eggs. Nests were avoided when potential avian nest predators, including cowbirds, were present. When nest contents were not visually inspected, 15-minute observations were made from a distance of 10-15 m to determine that the nest was still active based on adult activity.

Several behavioral measures were recorded during these 15-minute observations. These measures were tested for correlation to parasitism or predation risk. When approaching the nest, an adult usually lands in nearby vegetation and travels the remaining distance through the vegetation. This distance varies depending on either adult behavior or surrounding vegetation. The distance between the nest and where an adult drops into the vegetation when approaching the nest (drop distance) was recorded during nest construction and feeding of young. This distance was visually estimated in half-meter increments. Finally, the relative elusiveness of the adult when approaching the nest was recorded. Elusiveness was rated on a scale of 1 to 4 (Table 2-2). These measures, along with additional observations, were recorded on the nest card during each visit. Behavioral measurements were recorded for active nests monitored in 1998-2000; only nest activity was recorded in 1997. For purposes of data analysis of nest survival, a nest was assumed active if at least one egg was laid.

Table 2-2. Criteria for elusiveness rating of adult YWAR at the nest when the observer was nearby.

Rating	Criteria
1	A bird that flies directly or nearly so to the nest without regard for the presence of the observer.
2	A bird that drops into the vegetation before approaching the nest but otherwise does not hesitate.
3	A bird that is hesitant to approach the nest and is often difficult to follow to nest.
4	A highly elusive bird- rarely seen approach nest or will not go to nest when the observer is present.

A nest was parasitized if a cowbird egg(s) was observed in the nest. Cowbirds will lay eggs in a host nest during the final days of nest construction through the egg-laying stage (Robinson et al. 1995a). Nests that failed during egg-laying, where it was not known if it had been parasitized between checks, were excluded from analyses of parasitism rate and comparisons concerning parasitized nests.

If a nest failed before fledging young, the type of failure was record. Table 2-3 summaries the categories of nest failure observed. Nests were assumed to fail due to nest predation when the contents of the nest were missing and/or the nest was dislodged or torn. A nest was assumed to have failed due to abandonment if nest construction was not completed. Occasionally, a female would abandon the nest after laying one or two eggs. In these cases, abandonment was assumed the cause of failure since no other eggs were expected in the nest at the time the nest was checked. Failure due to burial of cowbird eggs was obvious. However, in a few instances egg burial was not discovered until nesting was complete and the egg(s) were found in the nest lining.

Table 2-3. Categories and number of nest failures for 347 monitored YWAR nests.

Failure type	N	Percent of failed nests
Predated	155	83.8
Abandoned	15	8.1
Buried	8	4.3
Weather/adult mortality	3	1.6
Unknown	4	2.2
Total	185	100

In only two cases was weather thought to have caused failure. In both, the eggs or young had fallen from the nest, which was apparently dislodged from the plant by wind or heavy rain. In another unusual case, a female was found dead on her nest with no noticeable harm. While the cause of her death is unknown, a severe storm did pass through the area the previous night.

Only a Blue Jay (*Cyanocitta cristata*) was actually observed depredating a nest, though Crows (*Corvus brachyrhynchos*) and Common Grackles (*Quiscalus quiscula*) were also seen in isolated instances flying by with eggs or nestling (species not known) in their bill. Also, both northern water snakes (*Nerodia sipedon*) and common garter snakes (*Thamnophis spp.*) were seen in close proximity to recently depredated nests with bulges in the body suggesting eggs or nestlings. Other potential nest predators seen or known to inhabit the area include the raccoon (*Procyon lotor*), skunk (*Mephitis mephitis*), white-footed mouse (*Peromyscus spp.*), eastern chipmunk (*Tamias striatus*), gray (*Sciurus carolinensis*) and red squirrel (*Tamiasciurus hudsonicus*), Cooper's Hawk (*Accipiter cooperii*), Great-horned Owl (*Bubo virginianus*), and Eastern Massasauga (*Sistrurus catenatus*). All sites were also inhabited by two other species of bird, the Gray Catbird (*Dumetella carolinensis*) and House Wren (*Troglodytes aedon*), which are not generally recognized as nest predators but are known to destroy nests (Spooner et al. 1996, Sealy 1989, Bellesisles and Picman 1986). Since the identity of nest predators cannot be accurately determine without direct observation much of the discussion concerning the predator community will be speculative.

Every effort was made to locate any re-nest attempt after failure. Female YWAR will commonly pull nest material from the previous nest to construct a replacement nest. The replacement nest is always built somewhere within the current territory. Construction of the re-nest typically begins only a day or two after failure of the previous attempt (pers. obs.). This information along with efforts to uniquely color band adults (see below) allowed for a confident determination of the identity of re-nest attempts. A re-nest was assumed to exist if the adult remained active on the territory for more than 10 days after failure of a prior nest. Most re-nests were found quickly during construction. Only a few re-nest attempts were not eventually located. In these rare instances, activity of the adults was still recorded to determine if a nest was eventually successful. Only when no adult activity was observed during several days of at last a half-hour of observation was nesting activity assumed terminated for the season.

Vegetation Assessment- When an active nest was completed, additional measurements of the nest site were made. These consisted mostly with assessing the concealment and vegetation around the nest and are summarized below. Measurements were performed promptly after either the nest failed or young fledged. By making these measurements soon after the nest was complete, the nest site conditions at the time the event occurred were more precisely ascertained. However, fledglings may remain in the proximity of the nest and females often use nest material from a failed nest to construct her replacement nest. Therefore, to avoid disturbing the birds these measurements were occasionally not performed immediately upon nest completion. Also, nest measurements were not made on buried nests until the subsequent nest attempt was complete. These measurements were recorded on the nest card.

Nest concealment was assessed two ways. One method followed a procedure commonly used in the literature and described by Martin and Conway (1995). This method has the observer subjectively determine the percentage of the nest that is concealed by vegetation. This is made from one meter away at nest level from the four cardinal directions and overhead. In many instances the overhead percent cover could not be viewed from one meter above due to nest height. Therefore, overhead cover was estimated at eye-level. This generally was not a problem since most often vegetation did not exceed more than a meter above the nest and was usually below eye level. Percent cover was recorded in 10% intervals. Nests had to be *at least* a certain percent cover to be rated at that percentage level. For example, if a nest was actually 47% concealed it was rated as 40% covered. This approach was used to minimize observer bias. A second measure of concealment followed the method used by Cresswell (1997). Here, a 3-inch piece of bright-pink flagging tape was placed on the rim of the nest. Using a 30-meter measuring tape, the distance (m) at which the colored tape was no longer visible was recorded at the four cardinal directions. For both methods, a mean percent cover or distance was calculated from the four cardinal measurements.

The height of the nest and nest plant (cm) were measured. The number of plant stems intersecting a plane through the nest rim in a 25 cm radius around the nest center was recorded as a stem density. This stem density was also used as an index to nest concealment in analyses. The percent cover of eight major plant categories (Table 2-4) found within a 2-meter radius around the nest was recorded. Percent cover was recorded in 10% intervals in the same manner as nest concealment. The total percent cover of all plant categories could not exceed 100%.

The number of snags and trees near a nest may influence vulnerability to nest predation or parasitism since it would provide perching locations for avian predators and cowbirds (Clotfelter 1998, Anderson and Storer 1976). Therefore, the number of snags and trees located within 10 meters of a nest were recorded. While trees greater that 10 meters away may also contribute to nest fate this distance was selected since in most cases trees within 10 m were still in the breeding territory boundary. A snag was any dead tree that stood at least 4 meters high. The number of live trees was recorded for two size classes: <15 and >15 cm DBH. Trees were any non-shrubby woody plant greater than 4 meters high. These nest site measurements were made in 1998 through 2000. This data was used to compare differences in vegetation structure in proximity to the nest to estimates of nest survival, and to determine if nest site preferences change for re-nests.

Table 2-4. Categories of vegetation that were quantified in vegetation assessment of a 2 meter radius around each nest.

Plant category	Description
Grass/sedge	All species of grasses and sedges.
Dog/willow	All species of willow and two species of dogwood- gray and red-osier dogwoods. Generally the two dogwoods species dominated this category.
Spirea	This is meadowsweet, the dominated low shrub preferred by YWAR's for nesting.
Forb	This category included any herbaceous plants excluding grasses and sedges, but including ferns.
Rose	This category included multifloral rose shrubs.
Other	This category included all other species of woody plants not in previous categories.
Dead	This category included any dead plant matter such as dried grass and sedge from the previous year or dead shrubs.
Water	This category included any standing water covering the ground

In the final year of the study, non-use nest sites for all active nests were selected and measured for vegetation at the same time as active nests. The following procedure was used to select these non-use nest sites. A random direction centered at the active nest was selected by tossing a stick into the air. The recorder would walk ten paces in the direction the stick pointed when it landed. If this placed the non-use site outside the known boundary of the territory then the opposite direction was taken. At this point, the height of the nearest plant was measured. Percent cover of surrounding vegetation within a 2-meter radius centered on the measured plant was recorded in the same manner as for active nests. Also in the same manner, trees and snags were counted in a 10 m radius. These non-use sites were used to evaluate the selectivity of nest sites by birds and for assessing the quality of nesting territories.

Color Banding- In addition to monitoring nest activity, efforts to capture and band breeding adults were made in 1998-00. Nylon mist-nets measuring 5-meters long and 2-meters high with approximately 3-cm mesh were used to capture adults. In 1998, 12-meter nets were also used as part of a separate study (Epp 1999). Adult males were drawn to the mist-net by playing a recording of the advertisement song near the net. A dummy bird carved from styro-foam and painted with appropriate markings was often placed in nearby vegetation to lure males. Females almost never respond to these recordings or dummy birds. Instead, females were captured by strategically placing the mist-net in common flight paths between vegetation. In some cases this meant placing the net close to the nest though rarely closer than 5 meters, and nets were not placed in locations that required significant trampling of vegetation to be set up. Nets were constantly monitored and birds removed immediately upon capture to avoid injury.

Upon capturing a focal bird, the bird was banded. A numbered U.S. Fish and Wildlife Service (USFWS) aluminum band was place on either the left or right tarsus depending on the year. Unique combination of two or three plastic color bands were also place on either tarsi. Color bands may be a single solid color or two colors split horizontally. Most often one band was placed on the same tarsus as the USFWS band and the other was place on the opposite tarsus. No more than two bands were placed on a single tarsus. Both adults of a breeding pair were given the same band combination.

The sex and age were recorded before a bird was released. Sex was easily determined from plumage differences. Male YWARs are bright golden-yellow and have striking chestnut streaks down the breast that are absent or faded in duller females. Age was determined using criteria described by Pyle (1997). These include comparing the contrast in color and feather-wear between the primary and greater covert feathers of the wing. The condition and shape of the tail feathers (rectrices) as well as length of the wing cord were also used. As recommended by Pyle (1997) and the Bird Banding Laboratory guidelines (Gustafson et al. 1997), age was categorized as second year (SY), after second year (ASY), or unknown (UNK) when feather condition was inconclusive. SY birds are in their second calendar year and are breeding for the first time, while ASY birds are assumed to have bred at least once before in a prior year. ASY birds have brighter less contrasting color between the primary and greater coverts of the wing, generally have longer wing cords, and have less-worn rectrices with more rounded tips. Age was used in comparative analyses of nest survival and nest attempts.

Both YWAR and COYE were banded and measured when captured. All other species that accidentally flew into the mist-net were immediately released. Banding was done under appropriate state and federal permits (Federal Permit No. 09633-P). Permission to handle live animals was also obtained from the Michigan State University Committee on Animal Use and Care (Application # 02/98-023-00). Most mist-netting effort was focused on capturing YWAR's. All COYE were captured accidentally during attempts to capture an adult YWAR. The color bands served to identify birds and aid in confirming the identity of replacement nests. Attempts to color band at least one member of each breeding pair were made, but not all birds were banded, especially in 1998. Some banded individuals returned in subsequent years increasing the proportion of banded birds in 1999 and 2000. Although not all breeding pairs were banded the identity of re-nests were confidently determined in nearly all cases through several criteria mention earlier.

Statistical Analysis- Nest survival was estimated using the Mayfield method (Hensler and Nichols 1981, Mayfield 1975, 1961). This commonly applied method uses the total number of nest failure events and nest exposure days to estimate the probability of failure as a daily rate or for the span of the nest cycle. Nest exposure days are the total number of days each nest was vulnerable to nest predation. I assumed that a nest was exposed to failure beginning on the first day of egg-laying. This method attempts to eliminate any bias resulting from the discovery of nests after egg-laying is complete since some failures in these cases may have gone undetected. However, most nests were located during either nest construction or egg-laying. If a nest was discovered during egg-laying, the total exposure days were calculated back to the day the first egg was laid under the assumption that one egg is laid per day (McMaster et al. 1999).

End dates of exposure were determined as follows. I assumed that nests were vulnerable to failure until fledging. If a nest fledged young between checks, the mid-point between checks was assumed the fledge date unless the hatch date was known. In the latter case, I assumed that fledging occurred 9 days following the hatch date (Ehrlich et al. 1988). Usually nests were checked every other day when fledging was anticipated and the exact day of fledgling could be easily determined. When a nest was depredated, the failure date was, again, assumed to have occurred at the mid-point between the present and previous check date. A nest was considered successful if it fledged at least one young, including cowbirds. These follow guidelines recommended by Mayfield (1975 and 1961). Survival or failure (predation) rate estimates and variances were generated using the program MICROMORT (v 1.3). Tests of significance between estimates of nest survival or failure rate were made by means of the Chi-Square test with the program CONTRAST (v 4.1) (Hines and Sauer 1989, Sauer and Williams 1989). Comparisons included survival for each nest attempt, each age class, and other comparisons as noted in Chapters 4 and 5. Unless otherwise noted, estimates of nest success or nest predation are presented for the span of the nest cycle.

The probability that a bird would re-nest following a prior nest failure at a given time (re-nest frequency) was estimated as follows. I first determined the number of birds whose nests failed during each of several 5-day intervals. I then counted the number of these birds that built a replacement nest. The re-nest frequency was the proportion of birds that re-nested out of those that failed during that interval. A bird was assumed to have re-nested if at least one egg was laid in a replacement nest. Birds in which it was unclear if they re-nested were excluded from this analysis.

Behavior data were summarized in the following manner. Drop distances and elusiveness rating were sub-categorized according to the nest stage at which it was measured (Building, Egg, or Nestling). When more than one measure of a single variable was taken during a particular nest stage, the mean was entered into the analysis. Visits were averaged per 15-minute periods. The number of visits by adults was recorded and sub-divided by nest stage as above. Not all measures were taken for all nests. For example, drop distance may have only been recorded during the building stage and not the egg or nestling stages or elusiveness rating was recorded only during the nestling stage. Because of this, traditional multivariate analysis such as logistic regression could not be used since incomplete cases would be excluded, thereby eliminating most nests, especially those that were depredated. Therefore, statistical analyses were made on each variable independently using a Kruskal-Wallis ANOVA for multi-way comparisons and Mann-Whittney U test for two-way comparisons.

A logistic regression analysis was used to determine which surrounding vegetation variables best distinguished various dichotomous dependent variables such as nest success (fledged versus predated) or age (ASY versus SY). A stepwise regression in the forward direction was implemented to find the best-fit model. Variables were included or removed from logistic regression models using a criterion of $P < 0.15$.

When appropriate, the Kruskal-Wallis Analysis of Variance test was made on data that were not normally distributed. When parametric tests such as ANOVA revealed the same conclusions as those of non-parametric tests, the parametric tests results were presented. Normality of data were verified by examining residual plots. Other statistical tests such as contingency tables were used as noted. All tests were two-tailed and conducted at the $\alpha = 0.05$ significance level. Statistical analyses were carried out using SYSTAT v.8.0 (SPSS 1998). Means are presented with standard error (SE) unless otherwise noted.

CHAPTER 3- ANALYSIS OF FIELD OBSERVATIONS

Fecundity and Life History- Nests of 201 female YWAR were monitored during the four-year study (Table 3-1). A total of 347 nests were discovered and monitored. We confidently located each nest attempt for all but 14 females (7 %). This was determined based on observations of activity on territories and the tracking of banded birds. Most females attempted two additional nests following nest failure of the first nest, but in three cases a fourth nest was also made. A total of 501 young fledged from these nests. Thus fecundity was estimated to be 2.49 young per female per season.

Table 3-1. Summary of the numbers of females, nests, and young fledged by year for all four sites combined.

Year	No. females	No. nests	No. Young Fledged	Fecundity per female	Fecundity per nest
1997	28	52	51	1.82	0.98
1998	51	86	123	2.41	1.43
1999	55	89	161	2.93	1.81
2000	67	120	166	2.48	1.38
Total	201	347	501	2.49	1.44

To evaluate the performance of the population, I estimated the fecundity necessary to sustain a population. This requires estimates of adult and juvenile mortality, which were not measured in this study. Instead, I selected estimates of 0.50 and 0.25 for adult and juvenile over-winter survival as conservative estimates (Ricklefs and Bloom 1977, Ricklefs 1973, Lack 1954). Using these values and assuming equal sex ratios, a population would need to produce 2.0 young per female to sustain a population. With the exception of 1997, the average young produced per female was 2.0 or greater (Table 3-1). Therefore, assuming that the estimates of adult mortality are accurate, this warbler population appeared to be sustainable and likely growing.

Fecundity per nest lies well below this threshold suggesting that nesting only once in a season will not sustain a population (Table 3-1). In fact, the estimate of seasonal productivity is approximately 40% greater than that estimated per nest. This difference indicates the contribution of re-nests to productivity. To directly identify the contribution of each nest attempt to seasonal fecundity, I determined the cumulative number of young fledged per attempt. From this, I determined fecundity for only first nests attempts, fecundity for first and second attempts combined, and so on (Table 3-2).

Table 3-2. Estimated cumulative young fledged per female by nest attempt. First nest attempts contributed the most to seasonal fecundity. Estimates of young fledged were determined according to the total number of young fledged up to that nest attempt. Values in parentheses are proportional contributions to total fecundity.

Year	Number of nest attempts		
	1	2	3[a]
1997	1.25 (0.69)	1.79 (0.29)	1.82 (0.02)
1998	1.51 (0.63)	2.18 (0.28)	2.41 (0.10)
1999	1.85 (0.63)	2.64 (0.27)	2.93 (0.10)
2000	1.67 (0.67)	2.31 (0.26)	2.48 (0.07)
All years	1.62 (0.65)	2.29 (0.27)	2.49 (0.08)

a. Includes 3 fourth nest attempts producing a total of 7 young.

In no year did this population produce a sustainable number of young per female by attempting only one nest. However, attempting one additional nest after failure did result in a sustainable productivity rate, again assuming that the mortality rates estimated above are appropriate for this population. At least 90 percent of all young produced came from the first two nest attempts (Table 3-2). Birds that attempt a third nest may do so as an insurance policy against a bad year when unexpected high adult or juvenile mortality occurs, or may be trying to maximize their individual fecundity.

Mean brood size (number of young fledged) for successful nests declines for each attempt (Figure 3-1, Table 4-3). A two-factor ANOVA (year and attempt, with sites pooled) revealed no significant effect for year but the decline in brood size by attempts was significant ($F = 12.745$, $df = 116$, $p < 0.001$). Pair-wise comparisons using Fisher's least significant difference (LSD) revealed a non-significant decline in brood size between first and second attempts ($p = 0.125$) but a highly significant decline in brood size from second to third broods ($p = 0.001$). Moreover, mean clutch size (number of eggs laid) was significantly reduced in each subsequent nest attempt (Figure 3-1, $F = 34.93$, $df = 107$, $p < 0.001$).

Mean brood size per nest attempt was slightly lower than clutch size in the same attempt (Figure 3-1). This is expected since not all eggs that are laid successfully fledge. No nestlings were ever found dead in a nest suggesting death by starvation was rare, while several instances of un-hatched eggs were observed. Thus, the difference between mean clutch size and brood size likely reflects hatch failure. Therefore, the observed reduction in broods by nest attempt is believed entirely the result of reductions in clutch size and not losses after laying.

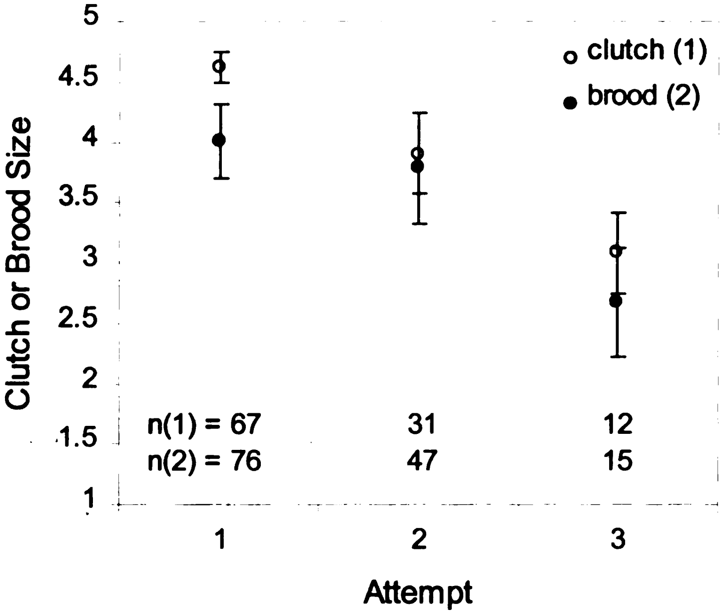


Figure 3-1. Mean clutch and brood size declined significantly with nest attempt.

Factors affecting clutch size is a richly studied topic in avian biology, and many hypotheses have been proposed to explain clutch size patterns (Murphy and Haukioja 1986). Most hypotheses interpret clutch size as a trade-off between maximizing fecundity and a variety of costs, which depend on the hypothesis. Examples include food availability, predation, or lifetime survival. The decline in clutch size with successive nesting attempts observed in this population suggests that there is a physiological cost to re-nesting, which limits the number of eggs a female can continue to produce. Similar reductions in clutch size have been observed in other YWAR populations (Mitra 1999). However, another study of this species found no significant reduction in brood size within the season (Goossen and Sealy 1982). This suggests that local variation in external resources, namely food, and deterioration of weather conditions, also contribute to this decline by limiting egg production (Smith and Andersen. 1982, Crick et al. 1993).

Brown-headed Cowbird parasitism rates on YWAR nests were relatively low and ranged from 0-33% between sites and years with an overall rate of 12.6 % (n = 310) for all years (Table 3-3). In contrast, parasitism on COYE was 41.2% (n = 17) over the same time period. In addition, more than half of accidentally discovered Swamp Sparrow and Song Sparrow nests had at least one cowbird egg and many of these had multiple cowbird eggs. This suggests that YWAR were not a preferred host despite references in the literature as such (Erhlich et al. 1988).

Reasons for the relatively low parasitism rate for YWAR despite frequent cowbird activity are unclear. Parasitism rates of YWAR have been measured at or near 50% in other localities in and near southern Michigan (Batts 1961, Berger 1951, DellaSala 1985, also see McGeen 1972) and as high as 80% in western populations (Tewksbury, pers. comm.). In addition, Freeman et al. (1990) found that Brown-headed Cowbirds are better at finding nests in marsh habitat with a high density of trees along the perimeter, which characterized all four sites used in this study.

Parasitism varied significantly between sites and was lowest at DW and highest at DE and RS ($X^2 = 14.748$, df = 3, p = 0.002). The difference in parasitism between DE and DW is particularly notable since these sites are located only 2 km apart. It is well documented that cowbirds are more frequent in fragmented landscapes near agriculture (Robinson et al. 1995b). The higher parasitism frequencies at RS, RR, and DE are likely due to their close proximity to agricultural lands and human habitation as compared to DW, which is more isolated (per. obs.). Individual differences in host preference by female cowbirds may also contribute to the variation between each site, and to the unexpectedly low parasitism rate observed for YWAR (Alderson, et al. 1999).

Table 3-3. Comparison of fecundity, predation, and parasitism by site, all years and attempts combined. Letters denote significant differences according to Chi-square tests.

Site	No. Females	Fecundity [1]	Predation	Parasitism
DE	51	3.14	0.394 [a]	0.247 [a]
DW	69	2.35	0.645 [b]	0.063 [b]
RS	16	2.00	0.543 [ab]	0.280 [a]
RR	65	2.26	0.709 [b]	0.190 [a]
All sites	201	2.41	0.546	0.126

1. Fecundity is calculated as the number of young fledged/ number of breeding females.

Nest predation rates between sites and years were variable and ranged from as low as 14.4% to as high as 78.3%. Overall, an average of 54.6% of nests were lost to predation. Predation rates were not significantly different between years ($X^2 = 4.197$, $p = 0.241$). However, predation did vary by site ($X^2 = 19.056$, $p = 0.0003$). This difference was mainly due to the significantly lower predation rate observed on DE compared to other sites (Table 3-3). A site-by-site comparison of overall predation and parasitism rates reveals that with the exception of DE increased parasitism is negatively correlated with fecundity (Table 3-3). Site DE had the highest mean productivity per female despite having the second highest parasitism rate, because of the low predation rate. No apparent relationship between predation and fecundity is evident from these sites. For example, while the lowest predation rate is associated with the highest fecundity, the second lowest predation rate is associated with the lowest fecundity.

Parasitized nests were 50% more likely to be depredated than non-parasitized nests (Figure 3-2). More frequent predation of parasitized nests seems likely due to several factors. Nests that were depredated or parasitized shared similar vegetative characteristics that link the two (see below). For example, nests placed near snags were more likely to be parasitized but were also more likely to be depredated. Also, cowbird nestling begging is loud and frequent (Dearborn 1998), and this may increase the risk of predation for parasitized nests (Briskie et al.1999, Leech and Leonard. 1997).

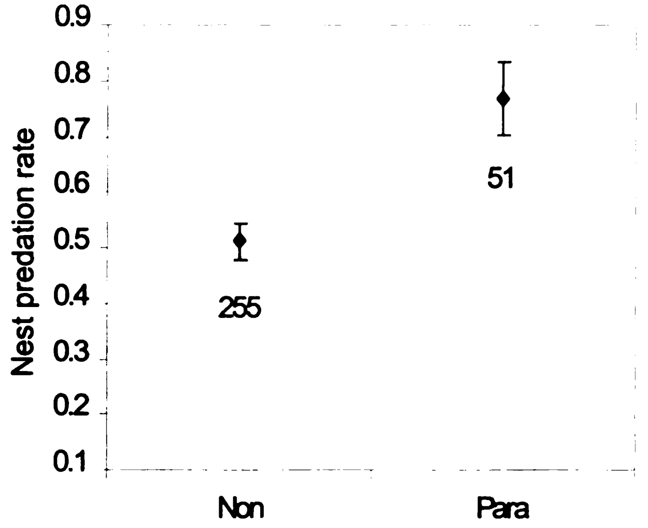


Figure 3-2. Comparison of nest predation estimates between non-parasitized and parasitized nests. Parasitized nests had a 50% greater risk of predation ($X^2 = 12.06$, $p = 0.0005$). Sample sizes are placed below standard error bars. Sites and years are pooled.

Variation exists in the literature whether parasitized nests are more or less likely to be depredated. For example, Strausberger and Ashley (1997) found no difference in nest success for six common hosts, while Payne and Payne (1998) and Weatherhead (1989) found greater predation on parasitized nests in the Indigo Bunting (*Passerina cyanea*) and Yellow Warbler, respectively. Thus, the correlation of nest predation and parasitism apparently varies depending on habitat and host species.

Those parasitized nests that did successfully fledge young averaged 1.56 young per nest. However, in two cases cowbird eggs failed to hatch in the nest. When these two nests are removed from the sample, the mean number fledged per nests drops to 1.11 young. Given that the overall mean brood size for successful non-parasitized nests was 4.11 young per nest (Table 4-3), successful parasitism reduced brood size by 73%.

Nest predation for re-nests was consistently higher compared to initial nest attempts (Figure 3-3). In general, predation on re-nests was 8-10 percentage points higher than initial nest attempts, which was not a significant difference for any given year but the overall trend was significant (paired t-test p = 0.004). Experimentation to determine the cause of this pattern is the subject of Chapter 5.

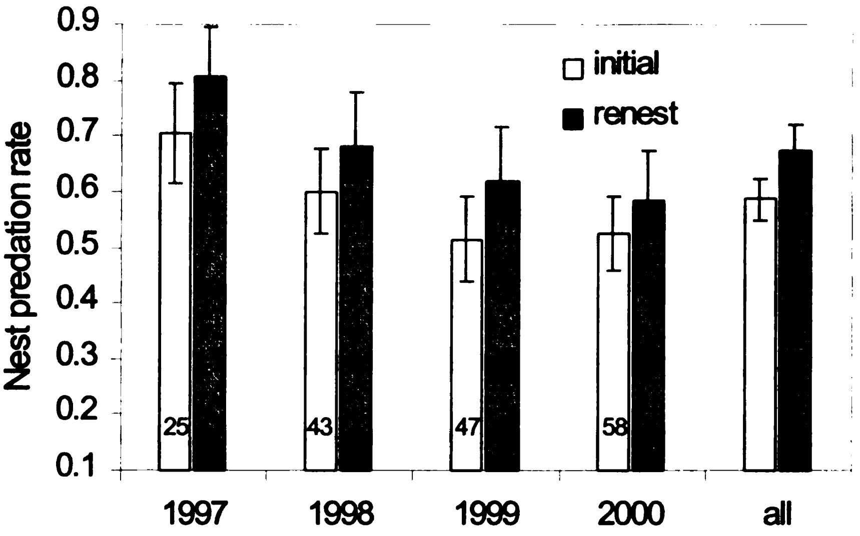


Figure 3-3. Mayfield estimates of nest predation were consistently higher for re-nests than for initial nest attempts, though not significant within years. Error bars denote standard error.

The potential for nest predation to enhance fecundity could exist only if the mean fecundity from parasitized nests which were not depredated was less than the mean fecundity of females who's parasitized nests were depredated. The difference between these two estimates is a measure of the beneficial effect of nest predation on parasitized nests, excluding any cost to nest predation on non-parasitized nests. Successful parasitized nests, including nests where cowbird eggs failed to hatch, averaged 1.56 ± 0.32 (± SE) young fledged, while females that escaped parasitism through nest predation averaged 1.53 ± 0.40. This suggests that this population could not gain in fecundity since females of depredated nests that contain cowbird eggs did not experience improved fecundity from subsequent re-nests. Failure to improve fecundity relative to successful parasitized nests probably resulted from increased predation on re-nests (Figure 3-3).

The total cost to predation can be evaluated by comparing the mean fecundity of successful first nest attempts to the total seasonal fecundity estimate for all nest attempts. The mean fecundity per female of successful first nests was 3.880 ± 0.112. This value is the expected fecundity if no predation was present while including parasitism. Comparing this value to the seasonal fecundity value estimated for the entire population (2.46 young/female) suggests that predation reduced fecundity by approximately 36% in this population. If we discard those nests that were parasitized, the mean fecundity per nest without predation is 4.11 young (Table 4-3). Comparing this value to the 3.88 young fledged per nest with parasitism suggests that parasitism reduced fecundity by only about 6%. This low reduction is undoubtedly due to the low overall frequency of parasitism observed in the population since the individual cost per nest was more than 70%.

Nest Placement- Nest concealment was measured three ways as described in Chapter 2. These were tape distance, coverage, and stem density. Poorly concealed nests should have greater tape distances, lower percent side cover, and lower stem densities around the nest. Therefore, tape distance is inversely related to the latter two measures. An ANOVA found that tape distance had a significant effect on nest fate (F = 6.252, p < 0.001). Pair-wise comparisons using Fisher's LSD revealed that tape distance was significantly greater for depredated nests compared to successful nests (Figure 3-4). Interestingly, mean tape distance for abandoned nests was similar to predated nests while buried and successful nests were similar. These patterns were consistent for side cover and stem density (Figure 3-4), suggesting that nest concealment may influence a bird's decision to abandon or bury a parasitized nest. However, sample sizes for abandoned and buried nests were too small to explore this further.

Parasitized nests have significantly less side cover and lower stem density compared to non-parasitized nests but they do not differ in tape distance (Table 3-4). These results suggest that proximate concealment of the nest influences vulnerability to parasitism but long distant concealment does not. Female cowbirds will search for nests by moving through low vegetation and can find nests by flushing adults from them (Strausberger 1998). Thus, the disparity in results of the three measures of concealment may reflect cowbird nest searching behavior.

Table 3-4. Comparison of marginal means for three measure of nest concealment between parasitized and non-parasitized nests.

Measure of concealment	Non parasitized nests		Parasitized nests		P-value (LSD)
	Mean	N	Mean	N	
Tape distance	4.21	139	4.55	35	0.433
Side cover	65.3	191	56.1	44	0.024
Stem density	24.2	190	20.8	44	0.047

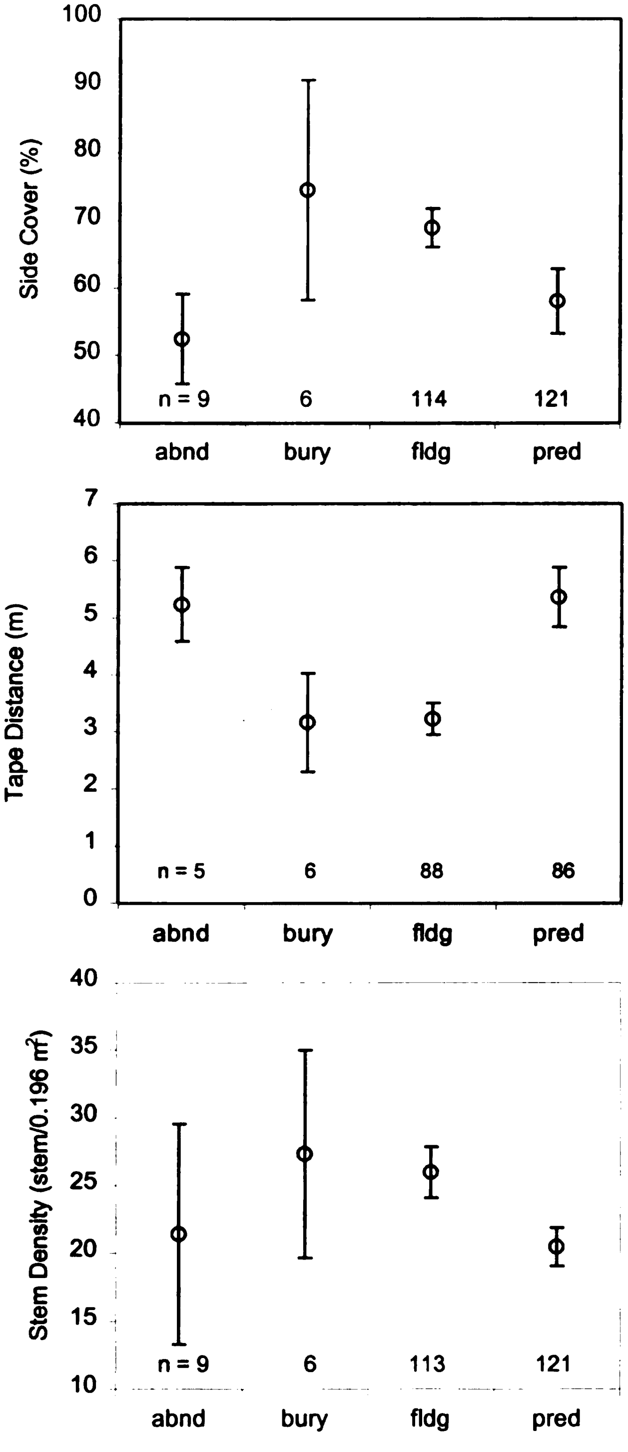


Figure 3-4. Three independent indices of nest concealment show that successfully fledged nests were more concealed than depredated nests. Error bars are 95% confidence intervals.

Parasitism events occur at the beginning of a nest attempt while concealment measurements were made after nest termination. Consequently, results may not reflect nest site conditions at the moment of parasitism. However, while Burhans and Thompson (1998) found nest concealment to vary with time, this pattern was not different between parasitized and non-parasitized nests. In other words, they found that all nests became less concealed with time. Because the change was consistent with nest type, comparisons using data collected after nest termination should still reflect real differences between them. Clearly, both nest predation and brood parasitism are influenced by nest concealment.

Results indicate no significant trend in nest concealment with respect to nest attempt. However trends were toward shorter tape distances, lower side cover, and less stem density with later nest attempts (Figure 3-5). The trend for tape distance is counter to that of the latter two measures. That is, shorter tape distance reflects greater concealment while lower side cover and stem density suggest less concealment. One plausible explanation for this result: Annual vegetation growth, especially of tall grasses away from the shrub patch where the nest is located could reduce tape distance measures in later nests. However, the proximate measures (side cover, stem density) trends toward lower concealment suggesting that adults select less concealed nest sites in later attempts, or that re-nests consist of a greater proportion of adults that selected less concealed nest sites. Again, this trend is not significant.

An ANOVA of overhead nest cover revealed a significant effect on nest fate ($F = 4.678$, $p = 0.003$) but not between nest attempts ($F = 0.543$, $p = 0.653$,) or parasitism ($F = 1.93$, $p = 0.147$). A contrast comparing overhead cover between successful and

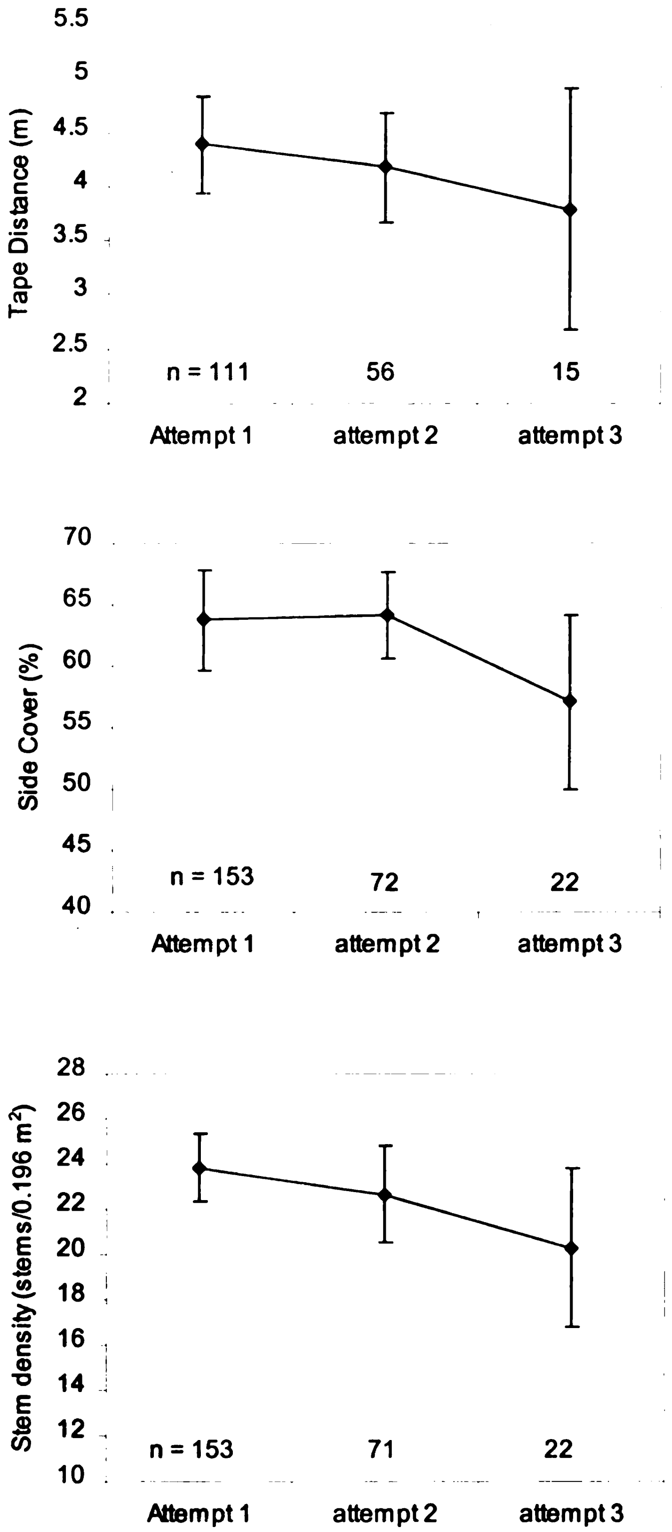


Figure 3-5. All three indices of nest concealment reveal no significant difference between nest attempts, though a slight downward trend is evident in all. Error bars are 95% confidence intervals.

depredated nests found successful nests had more overhead cover (F= 5.596, df = 234, p = 0.019). This pattern (Figure 3-6) was similar to that of all three measures of side cover (Figure 3-4), such that fledged and buried nests had the highest overhead coverage while abandoned and predated nests had the lowest.

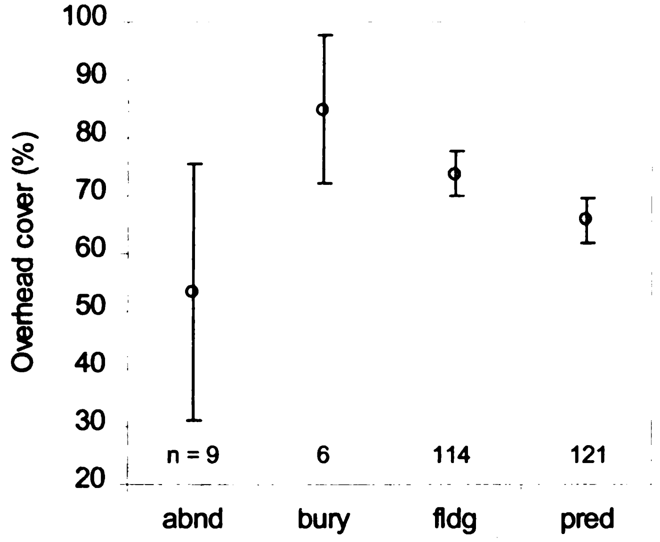


Figure 3-6. Successfully fledged nests had more overhead cover than depredated nests.

These results suggest that overall nest coverage in vegetation does influence nest success in this population. A review by Burhans and Thompson (1998) found few studies showing a relationship between nest concealment and either predation or parasitism. However, Martin (1992a) found in his review that more concealed nests were less prone to predation. Burhans and Thompson (1998) suggest that the influence of nest concealment on nest success seems to depend on nest predators. For example, Clark and Nudds (1991) found concealment to be important when avian nest predators were prevalent, but not mammalian predators. Best (1978) and Wray and Whitmore (1979) found no relationship between concealment and snake predation. Based on the condition of depredated nests and eye-witness accounts of predation, it appears that most nest predation was caused by avian predators such as the Blue Jay. Figure 3-6 supports this since overhead cover would seemingly only affect aerial predators.

In an analysis of nest height the best-fit model was an ANCOVA with plant height as a covariate. No significant difference in nest height with respect to nest fate, parasitism, or nest attempt was evident for all years and sites combined. There was a slight trend toward lower mean nest height in depredated nests (96.1 cm ± 2.26 versus 98.7 cm ± 2.40) and parasitized nests (92.8 cm ± 2.75 versus 97.8 cm ± 1.92) compared to successful and non-parasitized nests, respectfully. A trend toward placing re-nests slightly higher in nest plants compared to earlier attempts was also evident, but again, this was not significant. However, little variation in nest height exists in this population limiting the ability to detect a pattern. It seems that nest height has little influence on nest success or parasitism. This pattern is consistent with many studies (Smith and Arcese 1994, Best 1978, Payne and Payne 1998), though Dellasalla (1985) found parasitized YWAR nests to be lower.

The most common nest substrate was meadowsweet, followed by both species of dogwoods and then rose (Table 3-5). Nests placed in rose were significantly less likely to become depredated (Figure 3-7). A logistic regression analysis of proximate surrounding vegetation characteristics revealed that only the proportion of rose was significantly different between successful and failed nests (t-ratio = 2.612, p = 0.009, odds 1.022, Figure 3-8). Furthermore, non-use samples taken from territories of depredated nests were composed of a greater proportion of grass and sedge, and had less rose (Figure 3-9).

Table 3-5. The distribution of nest plants in a random sample of non-use sample sites compared to actual nest plants reveals that YWAR preferred meadowsweet and rose, with meadowsweet being the most common shrubby plant. See text for further discussion.

	Nest plant		Non-Use sample		Relative Difference (%)	Chi-Square P-value
Plant	N	%	N	%		
Meadowsweet	121	47.6	35	32.1	+32.6	0.014
Gray Dogwood	53	20.9	21	19.3	+7.7	0.579
Red Dogwood	38	15.0	19	17.4	-13.8	0.797
Rose	36	14.2	8	7.3	+48.6	0.086
Other	6	2.4	26	23.9	-89.9	< 0.001

Clearly rose was a deterrent to nest predators in this community. The dense and thorny characteristics of rose may prevent some larger predatory species, such as crows or jays, from reaching nests placed in or near rose patches. Also notable is a non-significant increase in the proportion of dogwood associated with depredated nests (Figures 3-8, and 3-9). Both species of dogwood shrubs tend to be less dense and thus provide less coverage around the nest.

The relatively low proportion of nests placed in rose is a reflection of the overall low frequency of rose on the sites. Relative differences provided in Table 3-5 are an index of nest plant preference by YWAR with respect to abundance of that particular plant species in the habitat as determined from non-use sampling. Positive values mean that this nest plant was preferred. Rose had the greatest positive difference showing that YWAR preferred to nest in rose but the low frequency of this substrate limited the overall proportion. Meadowsweet was also a preferred nest plant species. These preferences are also reflected in surrounding vegetation coverage between active nest plots (use) and non-use plots. YWAR placed nests near significantly more meadowsweet and less grass and sedge, forbs, and dead plant matter (Figure 3-10). They also preferred to nests near rose patches, but this was not significant. Preference by YWAR to place nests in rose and other low shrubs is consistent with other studies (Mitra 1999, Erhlich et al. 1988).

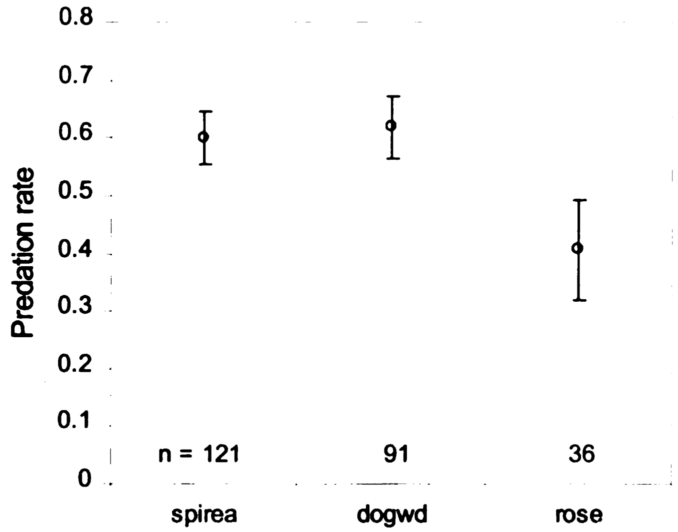
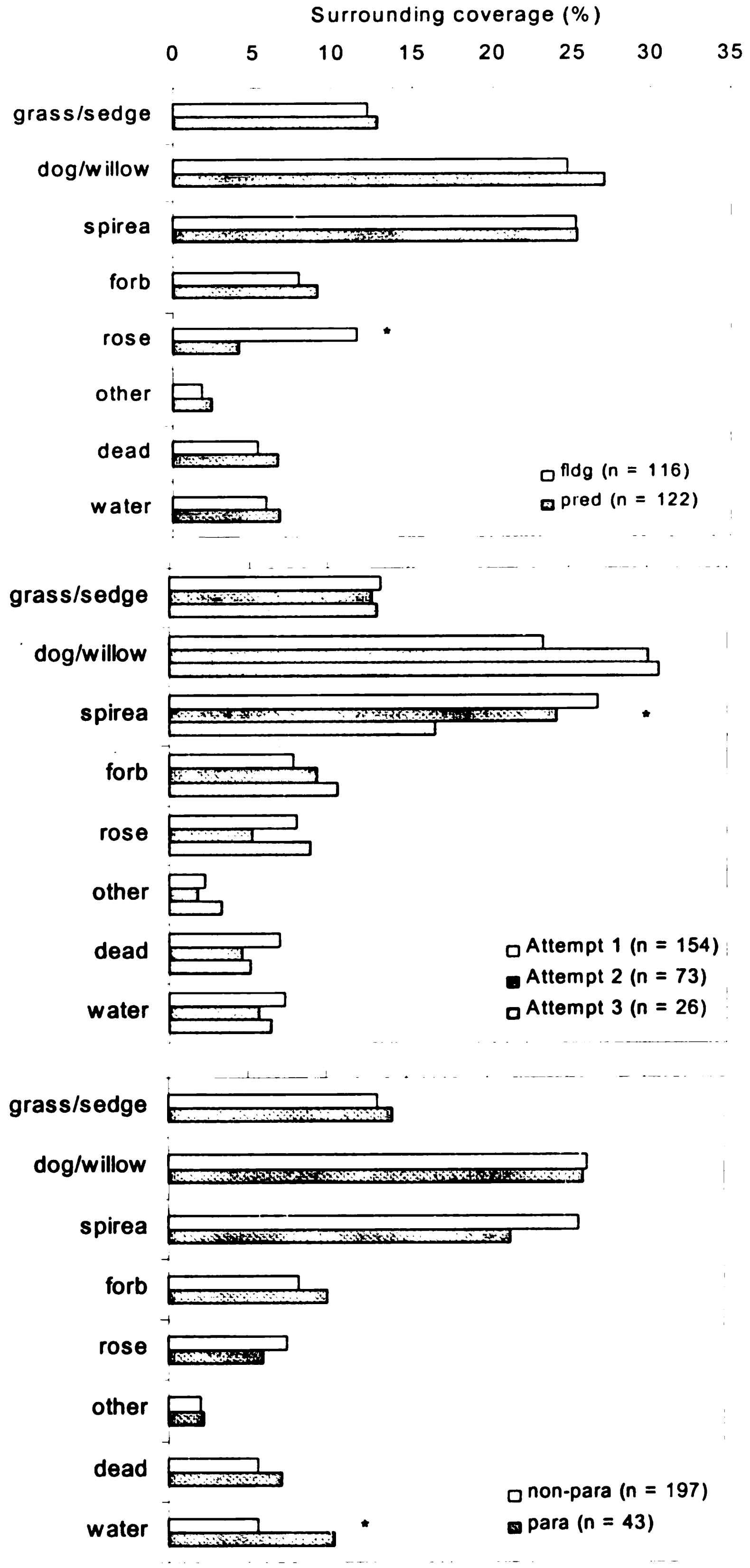


Figure 3-7. Nests placed in rose had significantly lower nest predation than nests placed in meadowsweet (spirea) or dogwoods ($X^2 = 4.48$, $p = 0.034$). Error bars denote standard error. Data are pooled for years, sites and attempts.

A two-way contingency table shows that nest plant preference did not change significantly with respect to nest attempt (Table 3-6). However, re-nests seemed more likely to be placed in dogwoods and less likely in meadowsweet. This pattern is also reflected in surrounding vegetation data (Figure 3-8). Logistic regression analysis of the various classifications of surrounding vegetation cover by nest attempt (3 levels) found the decline in meadowsweet coverage to be significant between the three attempts (t ratio = 2.339, p = 0.019). A more traditional logistic regression analysis coding the dependent variable dichotomously (first versus re-nests) found the percentage of dogwood (t ratio =

Figure 3-8. Three comparisons of percent coverage of surrounding vegetation in a 2 meter radius around the nest: Fledged versus depredated nests, by nest attempt, and non-parasitized versus parasitized nests. The percent cover of rose between fledged and parasitized nests was significantly different in a logistic regression analysis (t-ratio 2.612, p = 0.009, odds 1.022). A logistic regression with three possible outcomes for the dependent variable (nest attempt) found the change in meadowsweet (spirea) to be significantly different (t ratio 2.366, p = 0.019) with respect to nest attempts. A non-significant trend toward re-nesting in patches with more dogwood is notable. Only the abundance of open water was a significant predictor of parasitism (t ratio= 2.002, p = 0.045, odds 1.019).


Surrounding coverage (%)
0
5
10
15
20
25
30
35
grass/sedge
dog/willow
spirea
forb
rose
other
dead
water
*
fldg (n = 116)
pred (n = 122)
grass/sedge
dog/willow
spirea
forb
rose
other
dead
water
*
Attempt 1 (n = 154)
Attempt 2 (n = 73)
Attempt 3 (n = 26)
grass/sedge
dog/willow
spirea
forb
rose
other
dead
water
*
non-para (n = 197)
para (n = 43)

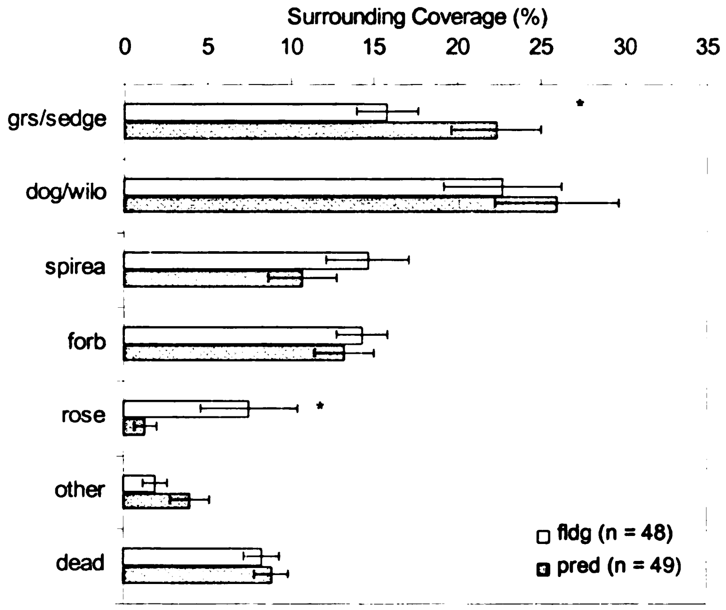


Figure 3-9. Logistic regression analysis comparing differences in surrounding vegetation characteristics of non-use samples found that territories of depredated nests were composed of a greater proportion of grass and sedge and had less rose ($p = 0.048$, and $p = 0.040$, respectively). Territories of depredated nests also have more dogwood and less meadowsweet (spirea), but means were not significantly different.

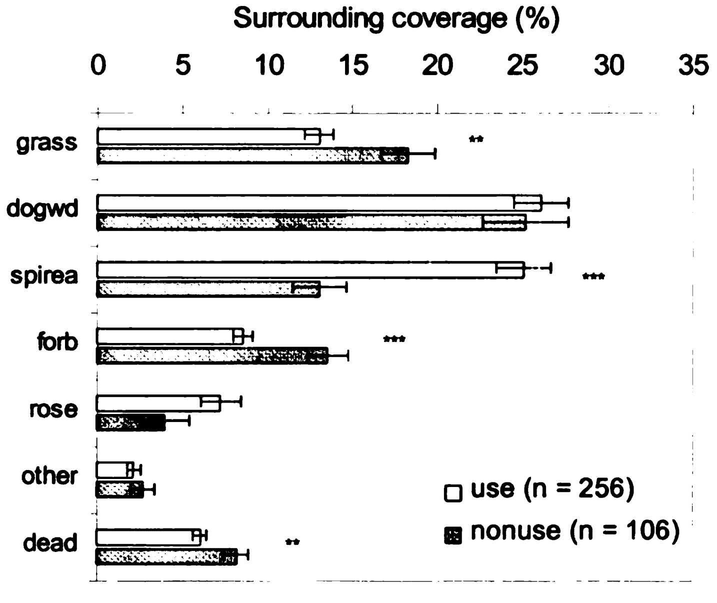


Figure 3-10. Logistic regression analysis of differences in surrounding vegetation coverage between active nest sites (use) and non-use plots suggests that YWAR select nest sites with more meadowsweet (spirea) and less herbaceous plants (*, $p < 0.05$; **, $p < 0.01$; or ***, $p < 0.001$). The difference in coverage of rose was marginally insignificant ($p > 0.108$).

–1.842, p= 0.065), dead plants (t ratio = 3.366, p = 0.018), and forbs (t ratio = –2.088, p = 0.037) to be significant or nearly so (Figure 3-11). Similarly, Mann-Whitney U tests of each vegetation variable versus nest attempt found dogwood (p = 0.046), forbs (p = 0.054), and dead (p = 0.071) to be significant or approach significance. As plant growth progressed during the season one would expect the percentage of dead plant coverage to diminish and the percentage of annual forbs to increase as observed. Therefore, only the increase in cover of dogwood/willow seems biologically important to nest placement.

Table 3-6. Nest plant preferences did not change significantly between nest attempts (Pearson's $X^2 = 8.22$, df = 8, p = 0.412). However, a shift occurs toward a greater proportion of later nests placed in dogwoods.

	Attempt 1		Attempt 2		Attempt 3	
Plant	N	%	N	%	N	%
Meadowsweet	79	51.0	33	45.2	9	39.1
Gray Dogwood	31	20.0	17	23.3	5	21.7
Red Dogwood	18	11.6	12	16.4	9	39.1
Rose	23	14.8	9	12.3	4	17.4
Other	4	2.6	2	2.7	0	0

Finally, a logistic regression found only water to be a significant predictor of parasitism (t ratio = 2.002, p = 0.045, odds 1.019, Figure 3-8). This relationship is likely due to correlation with density of snags. Most tall snags were in or near areas of standing water. In some habitats, Brown-headed Cowbirds are known to utilize snags as observation perches while searching for nests (Clotfelter 1998, Anderson and Storer 1976). Figure 3-12 shows that parasitized nests were associated with a significantly greater abundance of trees and snags. This pattern is consistent with other studies except that it has been suggested that cowbirds tend only to uses such perches in habitats that lack a closed canopy similar to the shrub swamps of this study (Brittingham and Temple 1996). Figure 3-12 also shows that depredated nests were associated with a significantly greater number of snags and small trees and that re-nests were associated with more snags. It would appear that the abundance of elevated exposed perches near nests has some influence on nest fate, suggesting that avian predators are common.

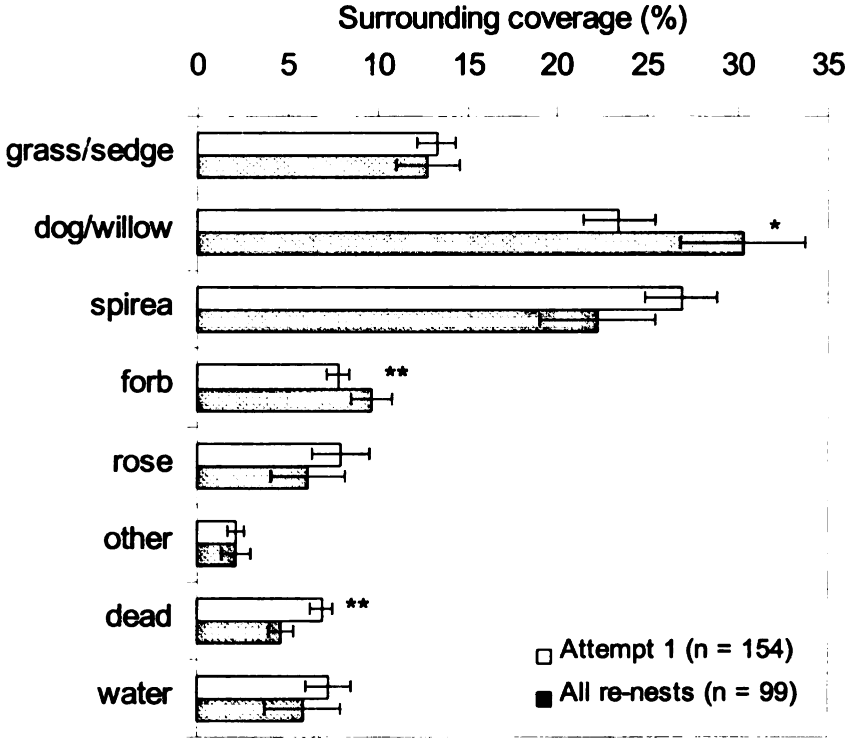


Figure 3-11. A dichotomous logistic regression of surrounding vegetation cover between first nest attempts and re-nests found the variation in coverage of dogwood/willow to approach significance (* $p < 0.10$) and found the difference in percent cover of forbs, and dead plant matter to be significantly different (**, $p < 0.05$).

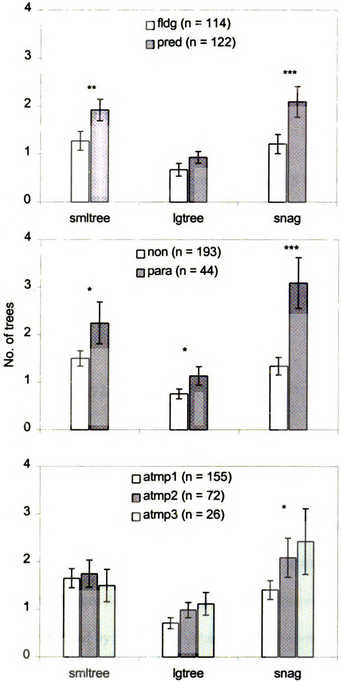


Figure 3-12. Predated and parasitized nests had more trees and snags nearby and later nests tend to be near more large trees and snags than earlier nest attempts. Compared are number of trees by category: small tree- smltree, large trees- lgtree, and snags, in a 10 m radius around the nest for: fledged versus predated nests, by nest attempt, and non-parasitized versus parasitized nests. Kruskal-Wallis One-way Analysis of Variance tests were used to test for significant differences. Asterisks signify level of significance (*, $p < 0.05$; **, $p < 0.01$; or ***, $p < 0.001$).

Parental age- Nests with both adults aged as second year (SY) were twice as likely to become depredated as nests where both adults were after-second year (ASY) (Table 3-7). In nests where only one adult was aged, ASY adults were also more successful than SY adults, but this difference was not significant (Table 3-7).

Table 3-7. Nests of adults, who had bred at least once before, ASY, were less likely to be depredated, than first time breeders, SY adults.

Parents	Age	N	Predation rate	X^2	p-value
Male and female	ASY	30	0.402	8.173	0.0043
	SY	10	0.825		
At least one[a]	ASY	92	0.538	1.949	0.1627
	SY	31	0.680		

[a] These are cases in which only one adult was sexed.

Contrasts of age and sex reveal that both SY males and females were significantly more likely to be depredated than their ASY counterparts (Figure 3-13, $X^2 = 7.119$, $p = 0.008$). These results suggest that older adults are more successful at avoiding nest predation. Consequently, re-nests were composed of a greater proportion of SY adults than original nest attempts (Figure 3-14). The greater nest failure rate of re-nests (Figure 3-3) is therefore partly explained by the greater proportion of inexperienced SY adults that were re-nesting due to prior nest failure. See Chapter 5 for further discussion of this. Brood and clutch sizes were not significantly different between adult ages.

Nests of SY adults were parasitized more frequently than ASY adults (Figure 3-15). However, Chi-square tests were not significant in either sex (males: $X^2 = 2.48$, df = 1, $p = 0.115$; females: $X^2 = 1.26$, df = 1, $p = 0.262$). Difference in males would approach significance in a one tailed test. An analysis of sample size suggests that this sample is insufficient to detect a significant difference (more than 400 nests would be needed to be 80% confident of detecting a difference). I have found only three other studies that compared host age to risk of parasitism (Smith and Arcese 1994, Payne and Payne 1998, Nolan 1978). Of these, only Smith and Arcese (1994) found a significant relationship. In contrast to my data, they found a greater risk of parasitism associated with older adults. Assuming cowbirds cannot discriminate hosts age, it is not likely that age is a direct determinate of parasitism risk but indirectly influences parasitism through factors that are correlated with age such as nest site characteristics.

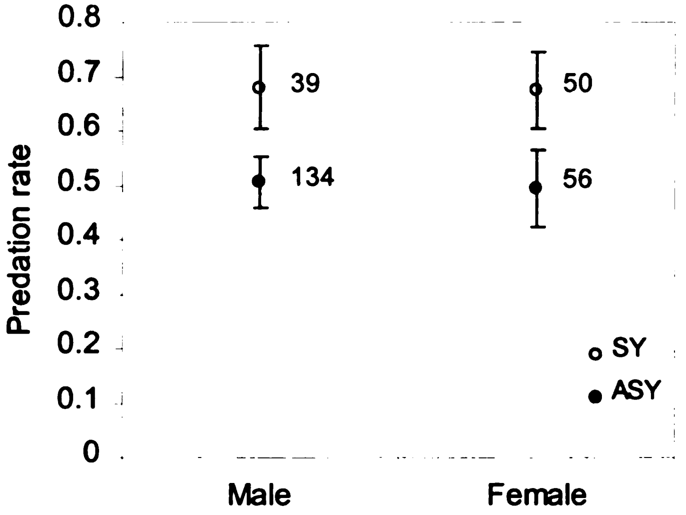


Figure 3-13. SY males and females had significantly higher Mayfield estimates of nest predation compared to their ASY counterparts ($X^2 = 7.119$, $p = 0.008$). Error bars are 95% confidence intervals; Sample sizes are included.

Logistic regression analysis of surrounding vegetation composition by age of nesting adults found that ASY females placed nests in patches with significantly more meadowsweet (t- ratio = 1.960, p = 0.050, odds 1.02, Figure 3-16). No other category of

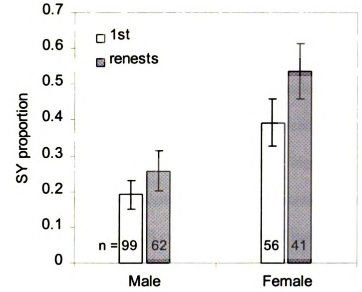


Figure 3-14. The proportion of SY aged adults in re-nests increased regardless of sex. However, the increase was not significant in either case. Pearson's Chi-Square results: $X^2 = 1.97$, df = 1, p = 0.16 and $X^2 = 0.98$, df = 1, p = 0.322 for females and males respectively. However, an analysis of both sexes combined was marginally significant ($X^2 = 3.455$, p = 0.063).

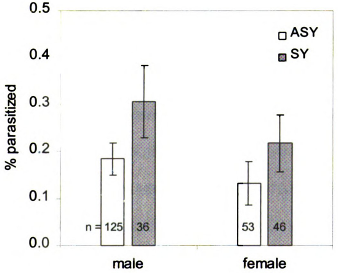


Figure 3-15. Nests of SY adults of both sexes were parasitized in greater proportions than their ASY counterparts. However, Chi-square tests were not significant in either sex (males: $X^2 = 2.48$, df = 1, p = 0.115; females: $X^2 = 1.26$, df = 1, p = 0.262).

vegetation was significantly different for female age, though nests of SY females tended to have more dogwood. No significant trend in surrounding vegetation in relation to male age was detected. Results of two-way contingency tables showed no significant difference in nest plant preference between ASY and SY males or females (Figure 3-17). However, nests of ASY females were more likely to be placed in meadowsweet while nests of SY females were more likely to be placed in gray dogwood.

Nests of ASY females were significantly more concealed from the side and had shorter tape distances (Table 3-8). Likewise nests of ASY males had significantly more side concealment, shorter tape distances and higher stem density (Table 3-9). Nests of both SY males and females had significantly more snags but only nests of SY females had significantly greater number of small and large trees, though males were only marginally insignificant (Table 3-8 and Table 3-9).

Given that nest success was related to nest concealment (Figure 3-4) and the number of nearby trees and snags (Figure 3-12), it seems evident that variation in territory quality or nest site selection between SY and ASY adults explains the difference in nest success observed with age (Figure 3-13). SY adults occupied territories that offer less concealment of the nest and had more trees and snags or were less skilled at selecting optimal nest site locations. It appears, then, that territory quality is a significant determinate of nest success and subsequent seasonal fecundity. Territories with a greater proportion of preferred nest plants, and fewer trees and snags performed better. It is also apparent that ASY adults occupied better quality territories. For example, nests of ASY adults had more meadowsweet (Figure 3-16) and thus more options for nest placement, and had fewer trees and snags (Tables 3-8 and 3-9). Therefore, shifts in nest placement

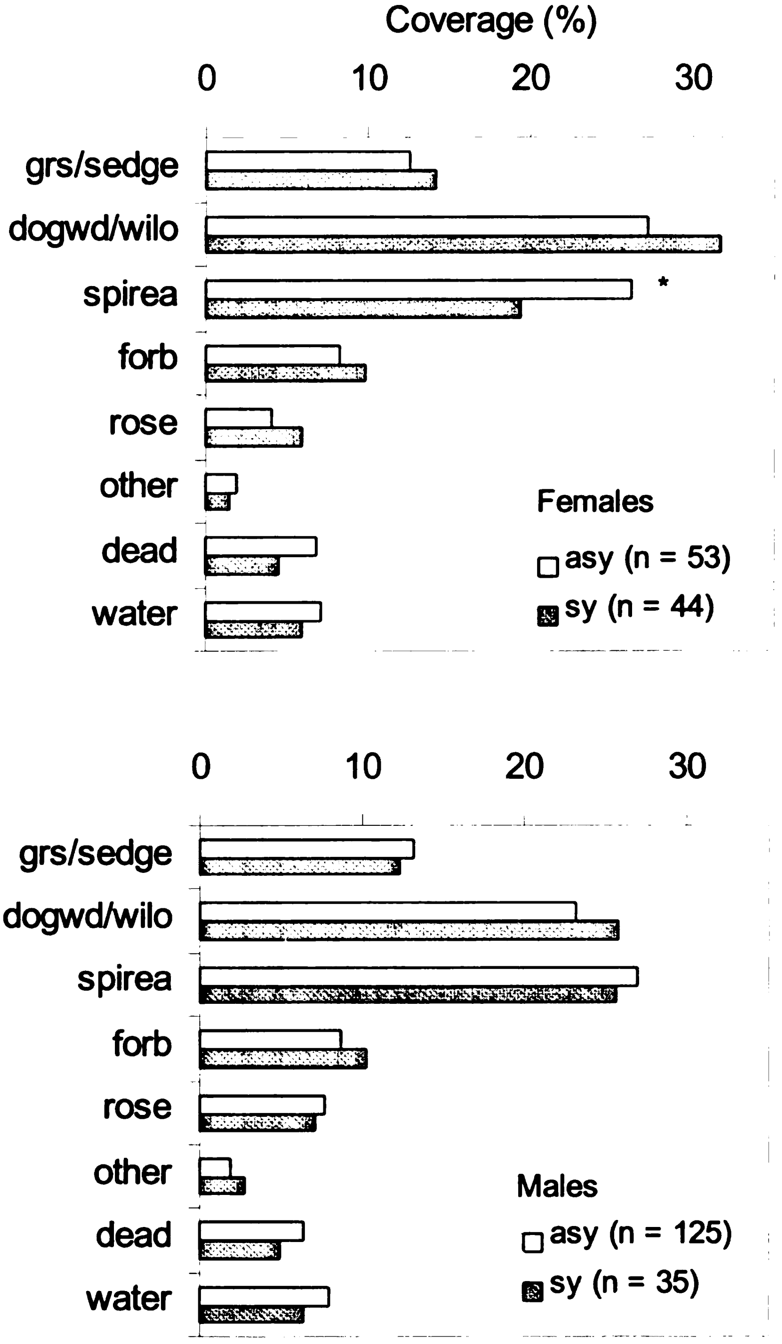


Figure 3-16. The percent cover of meadowsweet (spirea) was significantly greater in ASY females in comparisons of surrounding vegetation coverage by age and sex. Significance was determined using logistic regression (* $p = 0.05$).

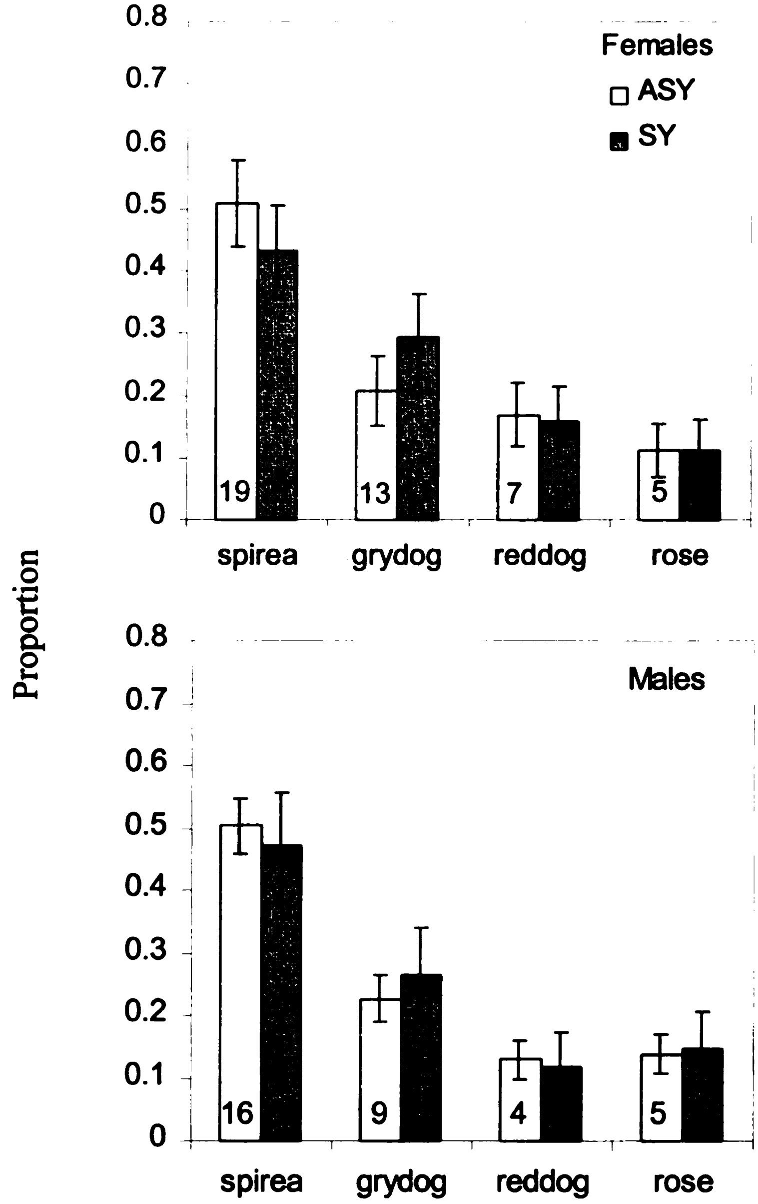


Figure 3-17. Two-way contingency table analyses between age and nest plant preference found no significant difference for females and males ($X^2 = 1.073$, df = 3, p = 0.784 and $X^2 = 0.263$, df = 3, p = 0.967, respectively).

Table 3-8. Comparisons of nest site characteristics by age of females show that nests of ASY females had more side cover, shorter tape distance, and fewer trees and snags than SY females.

	Females					
	ASY		SY		Kruskal-Wallis	
	N	Mean ± SE	N	Mean ± SE	X^2	P-value
Side cover	53	65.7 ± 2.24	43	56.9 ± 2.92	4.830	0.028
Overhead cover	53	67.8 ± 3.30	43	70.3 ± 3.64	0.279	0.597
Tape distance	41	3.67 ± 0.27	31	5.02 ± 0.47	6.792	0.009
Stem density	53	23.4 ± 1.23	43	21.5 ± 1.30	0.927	0.336
Trees <15 cm	53	1.19 ± 0.23	43	2.30 ± 0.48	4.17	0.041
Tress >15cm	53	0.62 ± 0.16	43	0.95 ± 0.16	5.23	0.022
Snags	53	0.98 ± 0.24	43	1.84 ± 0.36	5.11	0.024

Table 3-9. Comparisons of nest site characteristics by age of males show that nests of ASY males had more side cover, shorter tape distance, greater stem density, and fewer snags than SY males.

	Males					
	ASY		SY		Kruskal-Wallis	
	N	Mean ± SE	N	Mean ± SE	X^2	P-value
Side cover	125	66.9 ± 2.25	36	54.5 ± 2.78	11.40	0.001
Overhead cover	125	71.2 ± 1.93	36	67.8 ± 2.84	2.01	0.157
Tape distance	102	4.02 ± 0.22	31	5.00 ± 0.36	9.62	0.002
Stem density	123	24.6 ± 0.84	36	20.0 ± 1.43	7.50	0.006
Trees <15 cm	123	1.26 ± 0.20	36	1.92 ± 0.42	2.73	0.098
Tress >15cm	124	0.60 ± 0.09	36	1.14 ± 0.35	2.71	0.10
Snags	123	1.12 ± 0.16	36	2.58 ± 0.57	5.17	0.023

of re-nests observed for nest plant preference (Table 3-6), vegetation composition (Figures 3-8, and 3-10), and snags (Figure 3-12), appear to be the product of the greater proportion of SY adults (Figure 3-14) and not changes in individual nest site selection.

Parental Behavior- A comparison of behavior data between depredated and fledged nests was analyzed using Mann-Whitney U tests. Table 3-10 summarizes results of this analysis. Only behavior during the nest building stage appeared to be a significant determinate of nest success. Birds were more likely to succeed if they dropped further away from the nest when approaching, made fewer visits per 15-minute interval, and were scored more elusive. In general, successful adults were more elusive. However, if experiment-wise error is corrected using the Bonferroni correct alpha-value, only elusiveness during nest construction would be significantly associated with nest success.

A majority of nests failed within the first ten days of activity (Figure 3-18). Nolan (1978) observed snakes, chipmunks, and Blue Jays revisiting nests from which they previously consumed contents, and even observed predators revisiting nests found prior to egg-laying. This behavior has also been experimentally documented (Sonerund and Fjeld 1987), suggesting that some predators, especially avian predators, may first locate nests using parental activity during nest construction and return later to consume eggs.

No differences in parental behavior were detected between parasitized and non-parasitized nests or between nest attempts using Mann-Whitney U tests and Kruskal Wallis tests, respectively. ASY males visited nests more often (1.98 ± 0.177, n = 35) and dropped into the vegetation closer to the nest (2.31 ± 0.30 meters (m), n = 25) during the

Table 3-10. Comparisons of three measures of parental behavior by nest stage revealed that only parental elusiveness during the nest building was linked to nest predation. See Chapter 3 for an explanation of each variable. (A Bonferroni corrected critical value for significance is $p = 0.00556$).

		Fledged Nests		Predated Nests			
Stage	Variable	N	MEAN ± SE	N	MEAN ± SE	Mann U	p-value
Building	Drop (m)	47	1.94 ± 0.094	66	1.62 ± 0.108	1930	0.024
	No. Visits	64	3.36 ± 0.292	82	3.91 ± 0.211	2050	0.022
	Elusive	66	2.75 ± 0.087	86	2.36 ± 0.085	3564.5	0.004
Egg	Drop (m)	36	2.30 ± 0.195	27	2.56 ± 0.339	491.5	0.939
	No. Visits	31	1.39 ± 0.138	15	1.33 ± 0.179	236.5	0.920
	Elusive	74	2.92 ± 0.080	54	2.71 ± 0.129	2260	0.184
Nestling	Drop (m)	40	2.47 ± 0.237	2	2.00 ± 1.000	45.5	0.741
	No. Visits	53	1.62 ± 0.130	5	1.40 ± 0.245	143	0.761
	Elusive	83	3.15 ± 0.078	9	2.44 ± 0.377	516	0.049

nestling stage than SY males (1.13 ± 0.08, n = 8 and 3.67 ± 0.76 m, n = 6) (X^2 = 6.18, df = 1, p = 0.013 and 3.89, df = 1, p = 0.049 for visits and drop distance respectively). Males that occupied higher quality territories may find sufficient food more frequently and thus visited the nest more often, as observed. No behavior variables were significantly different among female age. These results indicated that behavioral differences and parental age were not strongly associated with each other. Therefore, age specific variation in nest success (Figure 3-13) appears not to be influenced by parental behavior but more likely by variation in territory quality (See chapter 5).

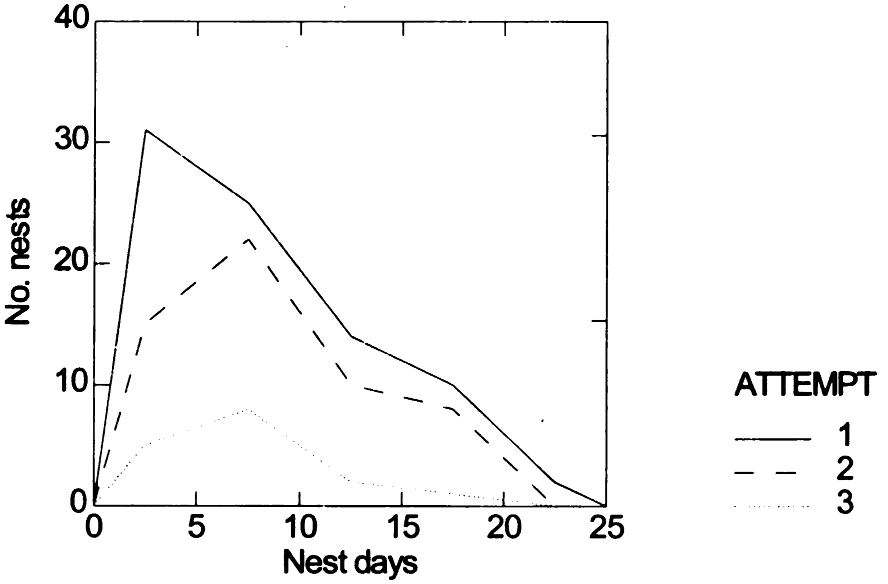


Figure 3-18. The distribution of number of nests depredated by nest days revealed that most YWAR nests were depredated during the first 10 days of the nest cycle regardless of attempt number.

Summary- Assuming the estimates of annual survival are appropriate, this YWAR population appeared to producing a sufficient number of young to be sustainable. This would not be the case had adults re-nested less frequently since re-nests contributed about

40% to seasonal fecundity. Overall nest predation was similar to that of most songbird populations, but the frequency of parasitism was unexpectedly low for Yellow Warblers. Those nests that were parasitized were 50% more likely to become depredated than non-parasitized nests; however, re-nests had consistently higher nest predation. Moreover, re-nests of depredated parasitized nests fledged equal or slightly fewer young than that of successful parasitized nests. Consequently, this population exhibited no potential to benefit from nest predation.

Nests placed in vegetation with more concealment did better than nests with less concealment. YWAR preferred to nest in rose or meadowsweet, and nests placed in rose or near rose patches were more likely to succeed, while nests placed near snags and trees were more likely to fail or become parasitized. Re-nests tended to have more snags nearby than first attempts. A trend toward a greater proportion of re-nests placed in or near dogwood species, which were associated with lower nest success, was evident.

Nest success also differed by age and re-nests consisted of a greater proportion of less successful SY adults. Both age classes also differed significantly in the composition of surround vegetation in proximity to nests. ASY adults placed nests near more meadowsweet, and had fewer snags, and possibly trees. ASY nests were also more concealed. Only parental behavior during the nest building stage significantly influenced nest predation. Male and female age did not differ with respect to behavior during nest building, indicating parental behavior did not influence nest success between ages.

CHAPTER 4 - THE MODEL

The Yellow Warbler field study provided many insights into nesting success and the impact of nest predation and brood parasitism. However, due to the overall low parasitism frequency and low nest success of re-nests, evidence of a relative benefit to nest predation was not found. The aim of this chapter is to address whether there exists any hypothetical conditions for which some level of nest predation might be better than no nest predation in a songbird *population*. To address this requires an examination of how various levels of nest predation affect seasonal fecundity across a range of parasitism levels and costs. Realistically, this cannot be done in a natural system. To do so would require manipulation of the frequency of nest predation and brood parasitism levels on various treatment populations, yet neither can be reasonably controlled in a natural breeding population. Therefore, simulation modeling was deemed the only appropriate means of exploring the interaction between these two phenomena.

There are two known quantitative models that predict avian productivity while independently accounting for the effects of predation and parasitism (Pease and Grzybowski 1995, Schmidt and Whelan 1999). Pease and Grzybowski's (P&G) model (1995) is a powerful, mathematically complex model that will generate fecundity estimates for a wide variety of conditions. Schmidt and Whelan (S&W) describe a mathematically simpler model consisting of a series of probability equations for all possible fates of a nesting female. Both explicitly and independently model nest predation and brood parasitism while allowing for re-nesting, and parameters can be readily manipulated. Therefore, either could be used to explore the relative effects of nest predation and brood parasitism. The S&W model was published following the end of this study and therefore was not available. Attempts were made to utilize the P&G model but failed mainly due to the complexity of their model and the fact that a number of parameters critical to the model could not be adequately estimated. Instead, I elected to design my own simulation model that would permit manipulation of parameters such as the frequency of nest predation or parasitism freely and would generate estimates of seasonal fecundity for a hypothetical population given essential life history information.

In this chapter, I present a dynamic model entitled FLEDGE which can simulate seasonal nesting cycles of single-brooding songbird populations. FLEDGE explicitly models the effects of nest predation and brood parasitism separately, and predicts the total number of fledglings produced by a female population for a single season. It is not specifically designed for predicting population growth across several years. Here, the model is used specifically to illustrate the interaction of nest predation and brood parasitism and to determine what conditions are necessary for nest predation to induce a relative increase in seasonal fecundity. The specific goals are outlined as follows: 1. Describe a quantitative population-based model that predicts seasonal fecundity given various conditions including brood parasitism and nest predation. 2. Test model performance against real field data. 3. Assess the relative impact of various levels of both brood parasitism and nest predation on seasonal fecundity using model simulations. 4. Evaluate the relative effects of selected conditional parameters on predicted seasonal fecundity with respect to the predation-parasitism interaction.

Model structure. - This simulation model was created using STELLA II Research® version 5.1.1 software (High Performance Systems 1997, Constanza et al. 1998).

STELLA is a graphically based program for creating dynamic mathematical models. A model is first constructed graphically in a form similar to a flow diagram. Then mathematical or logical relationships between flows and linked parameters are defined in a second layer. When a model simulation is executed, Stella calculates essential variables according to a time step process, recalculating variables at each time step as defined by the user. For example, consider a basic model of population growth. Stella would recalculate the size of the population for each defined time step (day, week, year, etc.) by taking the population size at the beginning of the time step and applying the birth and death rates, which can be fixed, time dependent, or density dependent according to model design. The model can be run for any number of time intervals and the result might be a plotted curve of population growth during that interval. A user can run a model only within the software program.

FLEDGE follows the basic structure described below and diagrammed in Figure 1-1. The parameters necessary to run the model are listed in Table 4-1. Initially a population of females, N, is uniformly divided so that they begin the nesting cycle over a 5 day period. As each set of females enters the nesting cycle, they are exposed to a brood parasitism frequency, p(t). This frequency is equivalent to the probability that a nest is parasitized and is commonly referred to by many authors as a rate. The parasitism frequency divides the population into those that are parasitized and those that are not. These two groups then continue temporally under a daily time step interval through the nest cycle: egg laying, incubation, hatching, and fledging. During each daily time step, a small proportion of nesting females are removed from this nest cycle according to a nest predation rate, d(t), which is converted to a daily survival rate (s) using the following equation,

$$s = \sqrt[(e+t_i+t_n)]{1-d(t)}\,, \tag{1}$$

where e is the clutch size, t_i is the length of the incubation period in days, and t_n is the length in days from hatching to fledging. The sum of these three parameters is the total number of days a nest is exposed to predation assuming one egg is laid per day. Again, the predation rate or frequency is equivalent to the probability that a nest is depredated. The daily failure rate is 1-s, and the number of females that fail (N_d) and are removed from the nest cycle during any given day is calculated as follows: $N_d = N \cdot (1\text{-s})$, where N is the number of females still actively nesting. To prevent rounding errors from propagating through the model, fractions of females are permitted.

The predation rate for parasitized nests, d_p(t), is adjusted by a measure of the difference in predation between non-parasitized and parasitized nests. This parameter, δ, is the proportionate increase (or decrease) in predation rate for parasitized nests. Thus, nest predation on parasitized nests is calculated using the following equation,

$$d_p(t) = d(t)\ (1+\delta). \tag{2}$$

When predation, d(t), is high or δ is large d_p(t) can become a frequency value greater than one. This is equivalent to nest predation being greater than 100%, which is illogical. To correct for this, the model truncates d_p(t) to the value of 1.0 when this occurs.

Abandonment is assumed to only occur during egg-laying for parasitized nests. The nest abandonment rate (a) is incorporated into the failure rate of parasitized nests during egg-laying, $d_p(\mathrm{t})_e$, according to the following equation,

Table 4-1. List of model parameters necessary to run a simulation.

Parameter	Symbol	Format	Stochastic	Time Dependent
Population size	N	Number of breeding females.	No	No
Predation rate	$d(\mathrm{t})$	Proportion of nests that fail due to predation (non-parasitized nests).	No	Yes
Parasitism rate	$p(\mathrm{t})$	Proportion of nests that are parasitized.	No	Yes
Abandonment rate	a	Proportion of parasitized nests that are abandoned.	No	No
Re-nest frequency	$r(\mathrm{t})$	Proportion of failed females that re-nest following failure.	No	Yes
Parasitism cost	c	Fractional reduction of brood size for parasitized nests.	No	No
Predation difference	δ	Fractional difference in predation rate for parasitized nests.	No	No
Clutch Size	e_i	Mean number of eggs laid in the i^{th} nest attempt.	Yes	No
Brood size	f_i	Mean number of young that fledge from successful non-parasitized nests for attempt i.	Yes	No
Nest building time	$\mathrm{t_b}$	Mean number of days spent building a nest.	Yes	No
Incubation time	$\mathrm{t_i}$	Mean number of days from laying of last egg to hatching.	Yes	No
Nestling time	$\mathrm{t_n}$	Mean number of days from hatching to fledging.	Yes	No

$$d_p(t)_e = d_p(t) + a[1- d_p(t)], \tag{3}$$

which takes the contribution of abandonment, a, relative to the predation rate, $d_p(t)$, and adds this to the total failure rate of parasitized nests during the egg-laying stage. Thus, the contribution of abandonment to total nest failure declines as nest predation increases.

Females that fail (N_d) can re-nest based on the number of previous attempts and a re-nesting frequency, $r(t)$, which is dependant upon the time in the nesting season the failure occurred. The number that re-nest, N_r, is determined from the calculation, $N_r = N_d\ r(t)$. A maximum of five nest attempts is allowed. Those that do not re-nest are removed from the model. Females that re-nest repeat the nest cycle and are exposed to parasitism and nest predation probabilities as before. Each female that successfully completes a nest cycle fledges a mean number of young (f_i) or brood size as defined by the user. Since it is possible for each nest attempt to have different clutch size each nest attempt has an independently defined mean brood size per female.

In FLEDGE, the mean number of young that fledge from parasitized nests (f_p) is calculated by adjusting the initial brood size (f_I) by a fractional cost to parasitism (c) using the following equation:

$$f_p = f_I \cdot (1- c). \tag{4}$$

This value, f_p, is used for all nest attempts unless the number of young that fledge from later non-parasitized nests (f_i) is a smaller value. In which case, the model assumes that there is no difference between the number that fledge from parasitized and non-parasitized nests for those nest attempts. After completion of the breeding season, the total number of fledglings of all nesting females is tabulated.

Each nesting attempt has the same structure as the original one with two exceptions. The number of females entering an additional nest attempt is determined by the number that fail in the previous nest attempt, and birds that fail in the fifth nest attempt do not re-nest. The user defines several parameters to run the model (Table 4-1). Life-history parameters can be modeled either as stochastic or deterministic values. During each time step of a simulation, Stella software algorithms select values for each stochastic variable. Values are selected from a normal distribution given the mean and standard deviation. Therefore, FLEDGE can function either as a partially stochastic (not all parameters are stochastic) or deterministic model depending on how parameters are defined by the user.

FLEDGE is not limited to constant probabilities of nest failure $d(\mathrm{t})$, parasitism $p(\mathrm{t})$, or re-nesting frequency $r(\mathrm{t})$. The user enters these probabilities as graphical functions versus time. The user plots a relationship between each of these parameters and day of the season, resulting in a plotted curve (for example see Figure 2-3). STELLA software automatically uses the value lying on this curve corresponding to a given day in the simulation. Consequently, changes in parasitism or nest predation during different times in the breeding season can be simulated. This is a particularly powerful feature of this model that gives the user great freedom when describing these parameters. For example, nest predation can be defined as a constant probability (a horizontal line) or as a declining probability (a downward sloping curve). In addition, daily estimates of these parameters are not necessary. Instead, one can estimate each parameter (if using field data) for a longer time interval such as by week. The median day in each interval is used to plot a curve through these points. STELLA automatically selects the appropriate daily value lying on this curve between the points.

Assumptions and limitations - FLEDGE assumes a maximum of five separate nest attempts. This limit may underestimate the maximum for some species (e.g., Nolan 1978) but the effect on the estimate of fecundity is likely small. For example, with a predation rate of 0.5, only little more than 6% of a population would attempt a fifth nest and only half of these would fledge young. After adding the effects of parasitism, abandonment, the cost to parasitism, and the reduction in brood size, the increase in fecundity contributed to fifth attempts will be minuscule. Some populations may attempt a maximum of less than five nests, as was the case for the Yellow Warbler. For such populations, the user can switch off later nest attempts to limit the total number a population will make.

FLEDGE is appropriate for only those species that fledge a single brood in a season. Successful females do not re-enter the nest cycle. However, general life-history parameters such as brood size and the length of nest stage are user defined. Thus, FLEDGE can be applied to several species, especially many of the small Neo-tropical migrants breeding in northern regions where more than one successful brood is rare.

Nests are assumed to be susceptible to predation from the beginning of egg-laying through the final day of the nestling stage, since this is the time period when a nest has consumable contents. Nest predation is not influenced by nest stage such that nestlings are no more likely to be depredated than eggs. There is some evidence to suggest that begging by nestlings may attract predators (Briskie, et al. 1999). However, this stage of the nest cycle had the lowest predation rate in my data (Figure 3-18). Therefore, I decided not to distinguish differences in predation between nest stages.

Only parasitized nests can be abandoned, and the frequency of nest abandonment is assumed to remain constant throughout the entire breeding season. A host will, therefore, abandon their final nest attempt even if doing so means zero fecundity. In other words, the model assumes that females have no knowledge of future nesting opportunities. If females can account for this we would expect to observe lower probabilities of abandonment for late nests. Graham (1988) found no such pattern for five host species. Moreover, in the current study there were at least two instances when yellow warblers abandoned their final nest attempt apparently due to parasitism.

The model does not explicitly include hatch failure, nestling mortality, or partial predation, where only a portion of the nest contents is consumed. The user accounts for such partial reductions in brood size by appropriately reducing the defined average number of fledglings per female (f_i) compared to the initial clutch size (e_i). Multiple-parasitism, where more than one cowbird egg is laid in a single nest is not explicitly modeled. Instead, the overall cost to parasitism including singular and multiple events is incorporated into the fractional cost to parasitism value (c).

A host is likely able to sufficiently nurture a predetermined number of young when parasitized, regardless of the initial brood size. For example, a warbler may only successfully raise two young when a cowbird is also present in a nest, and this will be the case if she had laid six or three eggs. Therefore, the number of young a host can fledge from parasitized nests (f_p) is assumed to be the same for all nest attempts even though a clutch reduction is likely to occur. However, it is possible that the clutch size or average brood size for a late nest attempt, f_l, is smaller than the brood size for parasitized nests. In this case, as stated earlier, the model automatically selects the lower value between f_l and f_p as the appropriate brood size.

As previously discussed, a variety of mechanisms can hypothetically cause differences in predation risk between nests that are parasitized and those that are not. These mechanisms are not likely to change or disappear within a breeding season. Therefore, the relative difference in predation between parasitized and non-parasitized nests (δ) is assumed to remain constant throughout the breeding season. However, the predation rate of non-parasitized nests, $d(\mathrm{t})$, can change with time and is used to calculate the parasitized nest predation rate, $d_p(\mathrm{t})$. Consequently, changes in these rates can occur but the relative difference between them cannot.

Females that re-nest are assumed to begin construction of the new nest the day after failure of the previous nest. Nolan (1978) has shown that most Prairie Warblers begin construction of re-nests between one and two days following failure. This pattern was also observed in the Michigan YWAR population (pers. obs.). Therefore, this assumption appears realistic. However, if this is not the case in a particular population under study, it can be corrected indirectly by extending the time spent building the nest ($\mathrm{t_b}$). One egg is laid each day such that the egg-laying stage lasts as many days as the size of the clutch. The initial number of females has no effect on other parameters in the model such that effects of population density cannot be simulated. Moreover, FLEDGE excludes events occurring before or after the nesting cycle and thus, does not deal with nest site availability or post-fledgling survival. Finally, there is no provision for adult mortality, and all females are assumed equal in their experience and nesting ability.

Validation. – Before FLEDGE can be utilized to explore the effects of nest predation and brood parasitism, model performance should be evaluated against real data to determine whether the model realistically describes seasonal fecundity given a realistic set of parameters. To do this, model estimates of total young fledged were compared to the actual number of young fledged using YWAR nesting data calculated from three field sites (RR, DE, DW, see Chapter 2). All the necessary parameters listed in Table 4-1 were calculated from the field data and are summarized in Table 4-2, 4-3 and Figure 2-3.

In order to appropriately validate the performance of a model, data used to compare model results must be independent from any data used to build the model (Grant et al. 1997). In this case, FLEDGE was designed according to general mathematical relationships focused on the probability events occur, such as nest predation. While field observations were used to understand the important parameters, no field data were incorporated into the permanent structure of the model or to define these mathematical relationships. Therefore, use of my own field data was deemed an appropriate validation of the model performance. Model estimates were compared to field estimated from each site and for all sites combined, with years pooled.

Estimates for entering the graphical inputs of nest predation and re-nesting frequency were calculated from weekly intervals. Weekly nest predation rates were estimated by counting the total number of nest exposure days and the total number of nests that failed due to predation within a given week. From this, weekly Mayfield estimates of nest survival or predation were calculated (Table 4-4, Mayfield 1961, Hensler and Nichols, 1981). Weekly re-nest frequencies were calculated by determining the ratio of nests that eventually re-nested versus the number of nests that failed in any

Table 4-2. Estimates of parameter values (± SD) used in model validation from Michigan YWAR field data pooled for all years.

Parameter	symbol	RR	DE	DW	all 3 sites
No. Females	N	65	51	69	185
Fledge/attempt	*f*	Table 4-3	Table 4-3	Table 4-3	Table 4-3
Clutch size/attempt	e	Table 4-3	Table 4-3	Table 4-3	Table 4-3
Parasitism[a]	p(t)	0.19	0.247	0.063	0.168
Predation	d(t)	Table 4-4	Table 4-4	Table 4-4	Table 4-4
Predation difference	δ	0.371	1.974	0.405	0.61
Parasitism cost	*c*	0.524	0.625	1.0	0.619
Re-nest Frequency	r(t)	Fig. 2-3	Fig. 2-3	Fig. 2-3	Fig. 2-3
Abandonment	*a*	0.27	0.27	0.27	0.27
Building time	t_b	4.0 ± 0.5	4.0 ± 0.5	4.0 ± 0.5	4.0 ± 0.5
Incubation time	t_i	11.0 ± 0.2	11.0 ± 0.2	11.0 ± 0.2	11.0 ± 0.2
Nestling time	t_n	9.0 ± 0.1	9.0 ± 0.1	9.0 ± 0.1	9.0 ± 0.1

a. Parasitism was held constant through time.

Table 4-3. Mean ± SD of the number of young fledged per successful YWAR nest attempt (f_i), by site, years combined. Estimates of clutch size were applied to all three sites.

Nest Attempt	RR	DE	DW	All 3 sites	Clutch size
1	4.20 ± 0.56	4.00 ± 0.60	4.19 ± 0.63	4.11 ± 0.60	4.4 ± 0.30
2	3.83 ± 0.58	3.44 ± 1.33	3.50 ± 0.67	3.53 ± 0.85	4.0 ± 0.50
3[a]	2.89 ± 0.75	2.50 ± 0.71	2.25 ± 0.96	2.67 ± 0.80	3.0 ± 0.50

a. Includes 2 successful fourth nest attempts from RR

Table 4-4. Weekly predation rates by site.

Site	Median Day						
	3.5	10.5	17.5	25.5	31.5	38.5	49.5
DE	0.0	0.230	0.350	0.198	0.493	0.263	0.795
DW	0.0	0.689	0.433	0.727	0.540	0.705	0.515
RR	0.791	0.623	0.643	0.722	0.719	0.535	0.242
All sites	0.419	0.529	0.488	0.603	0.590	0.599	0.488

given week. The model inputs for re-nest frequency, abandonment rate, and lengths of time for each stage of the nest cycle were the same for all sites since small samples sizes prevented estimates of these parameters within single sites. Stochastic parameters for mean brood size and nest stage lengths were used to predict seasonal fecundity. Ten simulation trials were performed for each site and for the combination of sites.

From each set of trials, a mean and 95% confidence interval were calculated and compared to the actual number of fledglings counted in the field. Based on observations in the field, I determined that all nesting attempts, except approximately 7% (14 of 201 females), were located during the field study. Therefore, it is likely that some fledglings were not counted. In an attempt to correct for this I multiplied this 7% of females by the average seasonal fecundity value per female associated with each site (Table 3-1). The result is an estimate of the average number of fledged young that went undetected. This number was then added to the total number of fledglings actually observed. Figure 4-1 plots these corrected estimates against the model estimates.

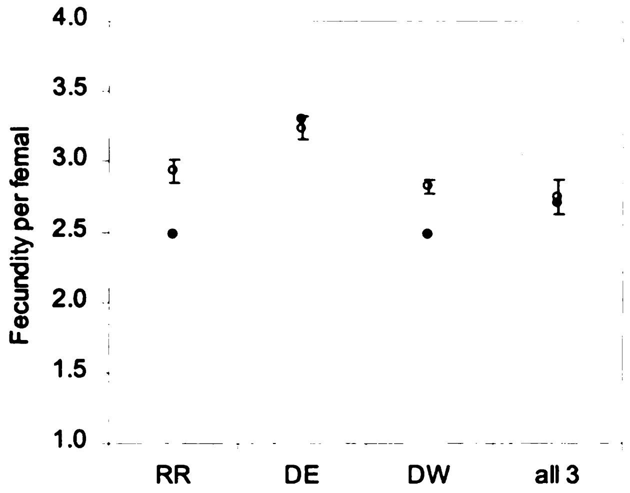


Figure 4-1. Model predictions of seasonal fecundity per site (open circles with 95% confidence intervals, n = 10) slightly overestimate actual field data estimates measured at each site (dark circles) except DE. This is significantly different only at RR and DW.

Fecundity measurements for DE and for all sites combined lie within the 95% confidence limits of model results (Figure 4-1). However, FLEDGE seems to overestimate the total young fledged especially at RR and DW. While it is possible that additional undetected fledglings may account for some of this difference, other conditions may also influence this result. For example, the same re-nest frequency function was used for all sites. However, in 1999, a total of seven females from RR and DW terminated nesting prematurely, possibly due to a heat wave that occurred the same week their prior nests had failed. The re-nest frequency for these two sites is lower for that week than was used. The lower frequency of birds re-nesting during that week would have undoubtedly lowered the total fecundity predicted by the model. Similarly, it is also likely that the abandonment rate, also estimated from all sites, was significantly different for these specific sites. Finally, estimates of weekly nest predation do have some error associated with them since the number of active nests in any given week can be small. Any error in these estimates may be reflected in these results.

As an additional test of model reliability I compared model estimates to Nolan's (1978) Prairie Warbler data. This is the only data set available that provided time interval estimates of parasitism (Nolan 1978: Table 126) and re-nest frequency (Nolan 1978: Table 149). Using this data set, I was able to find estimates for all parameters except δ, which I assumed to be equal to zero. I also assumed that nest predation remained constant. FLEDGE estimated fecundity as 1.99 young per female. This is lower than the 2.2 young per female estimated by Nolan but within the 95% confidence interval (1.9 – 2.5). However, the Prairie Warbler populations made more nest attempts, up to 7 attempts, and also had second broods. Therefore, we should expect FLEDGE to underestimate seasonal fecundity. According to Nolan's observations, 2% of females attempted more than 5 nests (Nolan 1978: Table 143). Therefore, the discrepancies in estimated fecundity is not likely caused by the failure to include these late nests in the model. I can estimate the contribution of second broods as follows. According to Nolan (pg. 418) only 7% of second broods were successful. Given an average brood size of 3.18 for all successful nests (Nolan 1978: Table 142), second broods would contribute an additional 0.22 young per female. Adding this to the estimate made by FLEDGE results in an adjusted result of 2.21 young per female, which is nearly identical to that observed by Nolan. Based on these results FLEDGE appears to accurately describe seasonal fecundity for natural populations.

Simulation experiments. - Several simulation experiments were performed to explore circumstances affecting the interaction between nest predation and brood parasitism. All simulations determined the number of young that successfully fledge during the season for a population of 100 females. Some simulation experiments used a stochastic model with the mean and standard deviations for clutch size, young fledged per female, and nest cycle lengths, provided in Tables 4-2 and 4-3 for the combination of sites. The purpose of using stochastic simulations was to gain an appreciation for the natural range of variability one might expect to observe. Except for the analysis of length of season, up to four nest attempts were allowed, with fecundity values for the fourth nest attempt equal to the third (Table 4-3). Other standard conditions are summarized in Table 4-5. In stochastic simulations, ten iterations for each combination of parameters were made.

Table 4-5. Summary of standard conditions for critical parameters used in simulation experiments.

Parameter description	symbol	Standard Value(s)
No. of Females	N	100
No. of nest attempts	n	4
Cost to parasitism	c	0.75
Differential predation	δ	0.0
Abandonment	a	0.10
Re-nest Frequency	r(t)	Figure 2-3
Clutch size	e_i	Table 4-3
Brood size	f_i	Table 4-3
Nest stage lengths	t_e, t_i, and t_n	Table 4-2
Simulation time	--	100 days

STELLA requires a specific length of time be defined for which calculations will be made. This time limit is not a model parameter but a specification of STELLA programming. This time was set at 100 days for most simulations though nearly all nesting was complete after 70 days according to the standard re-nest frequency. The 100-day limit was selected only for precautionary measures. As long as this time is greater than the time necessary for all nests to complete, it will not affect predictions made during a simulation.

Several sets of simulations were performed to examine specific manipulations of parameters on predicted seasonal fecundity. Table 4-6 summarizes these experimental simulations. Below are descriptions of each followed by their results. Means, 95% confidence intervals, linear regressions, and other statistical analyses, as described below, were performed using SYSTAT 8.0 (SPSS Inc. 1998). A two-tailed significance level of 5% was used in all cases.

Overall pattern- The first series of simulations evaluate the overall impact of various combinations of nest predation and brood parasitism on seasonal fecundity. Here, estimates of seasonal fecundity were made while the rates of nest predation and brood parasitism were systematically altered at 10 percent intervals. These simulations used the standard conditions, and both nest predation and brood parasitism did not change temporally through the season. Stochastic variables were not use in this set of simulations (i.e. only mean values were entered) resulting in a set of deterministic estimates.

Figure 4-2 summarizes these results in a surface plot. It is evident from this figure that both nest predation and brood parasitism negatively affect seasonal fecundity. However, the relative impact of one is closely dependent on the magnitude of the other. To assess the relative impact of nest predation or brood parasitism on seasonal fecundity one must compare the slope of the surface at the intersection of specific frequencies of each. Whichever axis has the steeper slope has the greater influence, or is more limiting, on fecundity. This varies depending on the particular combination of predation and parasitism frequencies. As a general rule, the slope is steepest for nest predation rates greater than 70%. Below this level, the slope for parasitism is similar or steeper than that for predation. The point where this switch occurs differs relative to the parasitism frequency. At lower parasitism, predation has a steeper slope at frequencies greater than approximately 40-50%, but at higher parasitism, this shifts to higher predation rates. Overall, brood parasitism has a greater negative impact on fecundity. For example, given these conditions, a bird with 60% predation and 30% parasitism will fledge on average 2.28 young while a bird with reciprocal conditions (30% predation and 60% parasitism)

Table 4-6. Summary of simulation experiments performed using FLEDGE. The tested condition is the main parameter of interested. Values used for this main parameter are provided. Alternate factors are other parameter(s) that were also altered or differed from standard conditions. A series of simulations for the set of main parameter values was repeated for each level of an alternate factor.

Tested condition	Parameter values	Alternate factors	Stochastic predictions
Predation vs. Parasitism	$d(t) = 0\text{-}0.90$ at 0.10 intervals	$p(t) = 0\text{-}0.90$ at 0.10 intervals	No
Declining parasitism [a]	$p(t) = 0.20, 0.40, 0.60,$ and 0.80	$d(t) = 0, 0.20, 0.40, 0.60,$ or 0.80	Yes
Differential predation	$\delta = 0, 0.25, 0.50,$ and 0.75	$d(t) = 0.20, 0.40,$ or 0.60 $p(t) = 0.60$ or 0.80	Yes
Declining predation [a]	$d(t) = 0.10, 0.30, 0.50,$ and 0.70	$p(t) = 0.60$ or 0.80 $\delta = 0$ or 0.5	Yes
Cost to parasitism[b]	$c = 0, 0.20, 0.40, 0.60, 0.80$ and 1.0	$\delta = 0$ or 0.5 $p(t) = 0.60$ or 0.80	Yes
Abandonment	$a = 0, 0.20, 0.40, 0.60, 0.80,$ and 1.0	$d(t) = 0.10, 0.30, 0.50,$ or 0.70 $p(t) = 0.20, 0.40, 0.60,$ or 0.80 $c = 0, 0.25, 0.50, 0.75,$ or 1.0	No
Length of season [c]	40, 50, 60, or 70 days	$d(t) = 0, 0.20, 0.40, 0.60$ or 0.80 $p(t) = 0, 0.40,$ or 0.80	No
Re-nest frequency [a]	Initial $r(t) = 0.30, 0.50, 0.70,$ or 1.00	$d(t) = 0, 0.30, 0.50,$ or 0.7 $p(t) = 0.40$ or 0.80	No

a. See Appendix A for specific values in declining trends of parasitism and predation, or for re-nest frequency (Tables A-C).
b. Predictions were made at $d(t) = 0$ and 0.30 to find the difference in fecundity at each value of c, see text for explanation.
c. Length of season was altered by reducing $r(t)$ from 1.0 to 0 during the final 5 days.

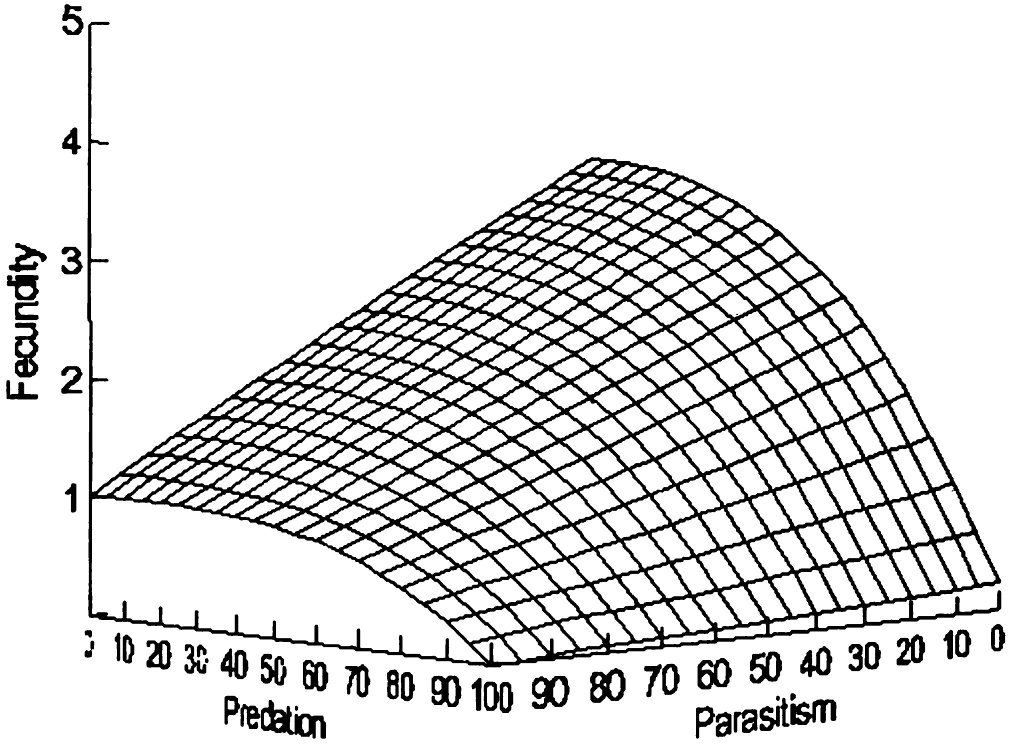


Figure 4-2. A surface plot of the mean number of young fledged per female revealed that predation and parasitism have an interaction. The rate of decline in fecundity as either factor increases in frequency varies with respect to the alternate factor such that the decline in fecundity due to predation is reduced as parasitism increases and vice-versa. A DWLS smoothing operation was used to produce this plot using SYSTAT 8.0 (SPSS Inc. 1998).

will fledge 2.10 young. Also, a bird with 80% predation and 0% parasitism does better than a bird with 0% predation and 80% parasitism (1.85 and 1.65 young per females, respectively).

In addition, the flattening of the fecundity surface at high parasitism and low predation along the predation axis indicates that nest predation has minimal effect on fecundity across a widening range of rates as parasitism increases (Figure 4-2). In other words, fecundity becomes less sensitive to nest predation as brood parasitism increases. For example, the average number of young fledged per female is practically equal whether she is exposed to 0% nest predation or 40% predation when parasitism is greater than 70%. Similarly, at high predation the effect of parasitism is also dampened, though a slight negative slope along the parasitism axis persists across the entire range of predation. Finally, no increase in fecundity ever occurs as nest predation increases from zero. Naturally, these results depend on the cost of parasitism, which in this case is a 75 % reduction in brood size. In any case, given these conditions, nest predation and parasitism interact antagonistically such that one reduces the effect of the other on fledgling production. Conditions exist at which increasing nest predation does not reduce seasonal fecundity. Similar conditions do not occur for brood parasitism.

Declining parasitism trend- The next set of simulations examined a declining brood parasitism frequency that begins the season at a maximum and declines eventually to zero as the season progresses. In this scenario, re-nest attempts will have a reduced probability of becoming parasitized. In many populations, parasitism by cowbirds is most intense early in the season and diminishes as the season progresses often terminating by early July (Scott 1963, Nolan 1978, Robinson et al. 1995a). Therefore, this declining function of parasitism reflects a pattern commonly expected in natural systems. The input values used for each declining parasitism function are provided in the Appendix (Table A-1). The slope of decline is not constant between different initial frequencies of parasitism. If this were the case at low parasitism, zero parasitism would quickly be reached in the season. Even when parasitism is low, it is not likely that the declining frequency of parasitism events would completely vanish early in the season. Instead, I defined the decline in parasitism such that the rates of decline are a constant percentage relative to the initial frequencies (Table A-1). All other parameters were held at standard conditions. The impact of a declining parasitism frequency was tested across a range of constant predation rates.

Figure 4-3 summarizes these results, which are similar to the overall pattern using constant parasitism shown in Figure 4-2. As before, at high levels of parasitism, nest predation, at low frequencies, does not significantly reduce fecundity. This trend is only slightly different from that seen in Figure 4-2. The main difference being that there is a slightly expanded range of predation at which no effect to nest predation exists. In general estimates of fecundity with constant parasitism lie within 95% confidence intervals, except at high parasitism and nest predation. The latter cases are probably due in part to the greater change in absolute parasitism frequency for higher parasitism as a result of the percent of decline used (Table A-1). Since predictions generally were not significantly different from those using a constant parasitism, this more realistic declining parasitism trend was used in all remaining simulations.

Changes in nest predation patterns- Simulations were also performed to explore changes in seasonal fecundity for different patterns in nest predation. One series of simulations tested the effect of a difference in predation between parasitized and non-parasitized nests such that parasitized nests had a 25, 50 or 75% greater risk to nest predation ($\delta = 0.25, 0.50$ or 0.75). Fecundity estimates were generated for nest predation at 20, 40, and 60% and at two levels of parasitism (60% and 80%).

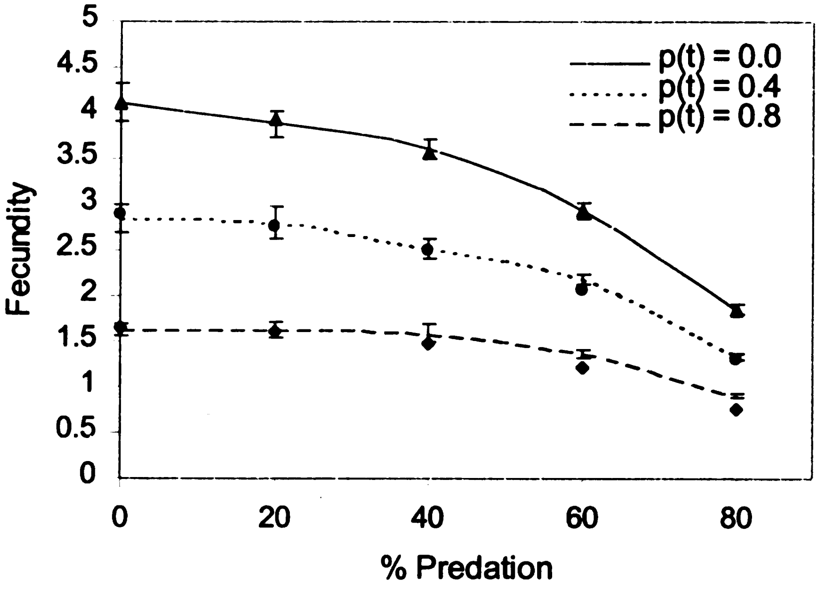


Figure 4-3. This figure compares fecundity estimates versus nest predation for a population for which the frequency of parasitism does not change throughout the season (solid points) with a one where parasitism declines as the season progresses (line with 95% confidence intervals, n = 10). Only at very high frequencies of parasitism and predation do these two population differ significantly in fecundity.

Figure 4-4 summarizes the results of this analysis. With the exception of when parasitism is 80% and predation is 60%, increasing predation on parasitized nests results in a significant linear increase in fecundity. The change is small, generally less than 0.15 young per female between $\delta = 0$ and 0.75. The other effect of increasing predation on parasitized nests is that a small benefit to nest predation occurs (Figure 4-5). A positive change in fecundity relative to zero predation occurs at both 20 and 40% predation

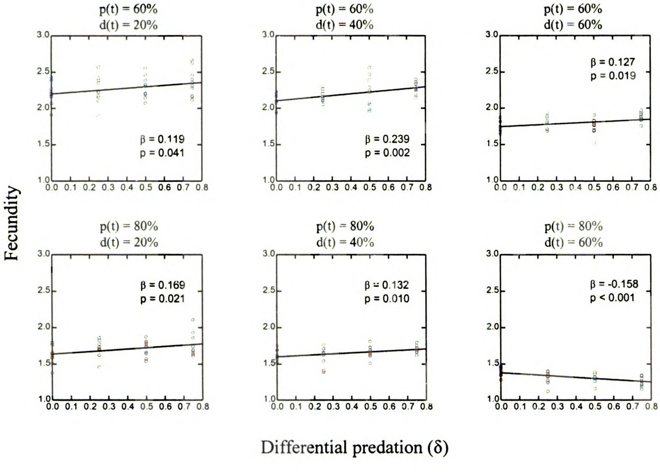


Figure 4-4. Increasing the proportionate difference in predation (δ) of parasitized nests relative to non-parasitized nests generally results in significant but small linear increases in fecundity regardless of the parasitism, p(t), or predation, d(t) rates. This trend reverses only when both rates are high. Regression coefficients (β) and significance values are provided.

(Figure 4-5). While the magnitude of this positive change is similar in these stochastic results, the change is not significant at 60% parasitism but is significant at 80% parasitism. This result confirms that intermediate nest predation can cause a small positive change in seasonal fecundity under intense parasitism.

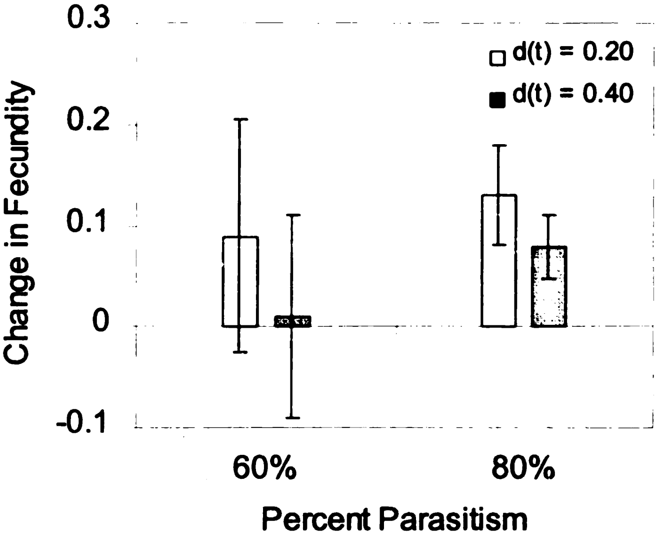
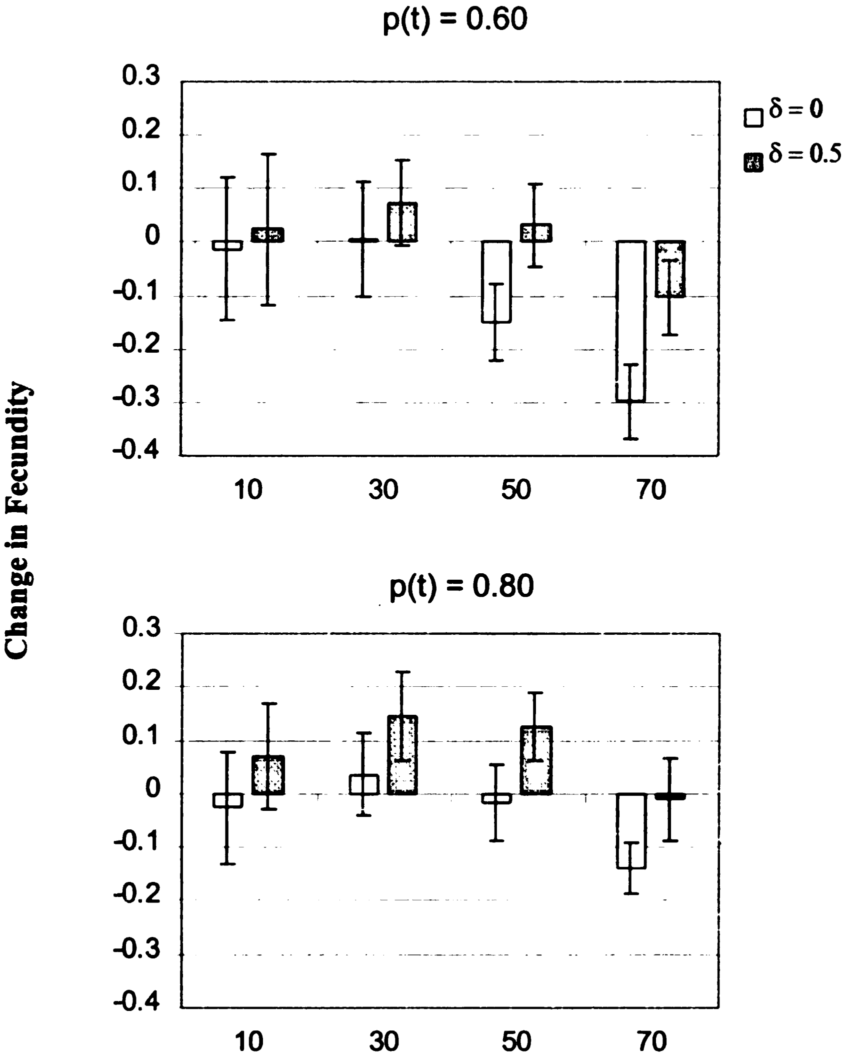


Figure 4-5. Shown here is the change in fecundity relative to zero nest predation at two levels of parasitism and nest predation, d(t), when δ = 0.75. The change in fecundity is positive for all four combinations of predation and parasitism. This change is greater at a low predation rate than at a moderate level and is significantly greater than zero only at 80% parasitism. Error bars are 95% confidence intervals (n = 10).

In another series of simulations, the frequency of nest predation was gradually decreased over the breeding period to half the initial frequency, simulating a reduced risk to nest predation for re-nest attempts. Values used in the graphical input of this declining predation trend are provided in Table A-2 of the Appendix. Similar to the declining parasitism functions, the rates of decline in predation are a consistent percentage relative to the initial frequencies. The effect of decreasing nest predation was tested over a wide frequency range of predation, at 60% and 80% parasitism, and δ = 0 and 0.50.

Figure 4-6 summarizes the results of this analysis by plotting the change in fecundity relative to zero predation. At $\delta = 0$ and 60% parasitism, there is no significant change in fecundity at predation frequencies of at least 30%. At $\delta = 0$ and 80% predation there is a slight non-significant positive change in fecundity at 30% predation and the zero effect exists at 50% predation. If a differential predation effect is included, $\delta = 0.5$, there is no significant difference in fecundity for predation as high as 50% when parasitism is 60%. However, at 80% parasitism, a significant increase in fecundity exists at both 30% and 50% predation. Moreover, there is no difference in fecundity at a predation frequency of 70%. In other words, the mean number of young fledged per female does not differ whether nest predation is zero or 70%, when initially 80% of nests are parasitized, parasitized nests have a 50% greater risk of failure, and re-nests have greater nest success. Increased success for re-nests is an important and powerful condition in determining the outcome of the predation-parasitism interaction.

Cost to parasitism- Previous simulations determined that a positive change in fecundity or non-negative effect to nest predation can exist at moderately low predation rates when parasitism is frequent. These results were based on a 75% reduction in brood size (or cost to parasitism) for parasitized nests. The next series of simulations attempts to examine what effect the cost to parasitism has on these results. Here, I determine the level of cost to parasitism that must exist for it to pay on average to have a parasitized nest depredated. This was done by systematically altering the parasitism cost value (c). For each value, mean estimates of total young fledged were generated for 0% and 30% constant nest predation. For the conditions simulated, 30% nest predation corresponds closely to the maximum positive change in seasonal fecundity as discovered from



Declining Predation (%)

Figure 4-6. Positive mean changes in fecundity per female relative to zero predation are enhanced by a declining predation rate and when δ is greater than zero. The magnitude of this change is greater at high parasitism rates, p(t). Furthermore, the range of predation at which a positive or no change in fecundity occurs is greater compared to previous results where predation was held constant through time. Error bars denote 95% confidence intervals.

previous simulations. This was repeated for four treatments, 60 and 80% declining parasitism and $\delta = 0$ and 0.5. The frequency of nest predation was held constant through the season and all other conditions were set at standard levels.

Table 4-7. Estimates of the minimum cost to parasitism for a positive change in fecundity to exist at a 30% predation relative to 0% predation. Estimates are given for two levels of parasitism and differential predation. Values were calculated by finding the x-intersection from regression equations derived in SYSTAT.

	Differential predation value (δ)	
Parasitism	0	0.5
60%	108%	79%
80%	79%	69%

The difference in total young fledged between 0% and 30% nest predation was calculated. These differences were plotted against the corresponding cost to parasitism value (Figure 4-7). The intersection of the line at the x-axis (cost to parasitism level) indicates the minimum cost to parasitism that must exist for predation to lead to an increase in fecundity for a population under the identified conditions. The values at this intersection were calculated from a linear regression analysis for all four treatments and are provided in Table 4-7. Results indicate that a relatively large cost to parasitism must exist for nest predation to increase fecundity. A higher cost is necessary when the frequency of parasitism drops and when parasitized nests do not have greater predation.

Nest Abandonment- Another set of deterministic simulations explored the effect of nest abandonment. Here, the level of abandonment was altered at 20% intervals while nest predation was held constant at four levels (Table 4-6). The frequency of brood

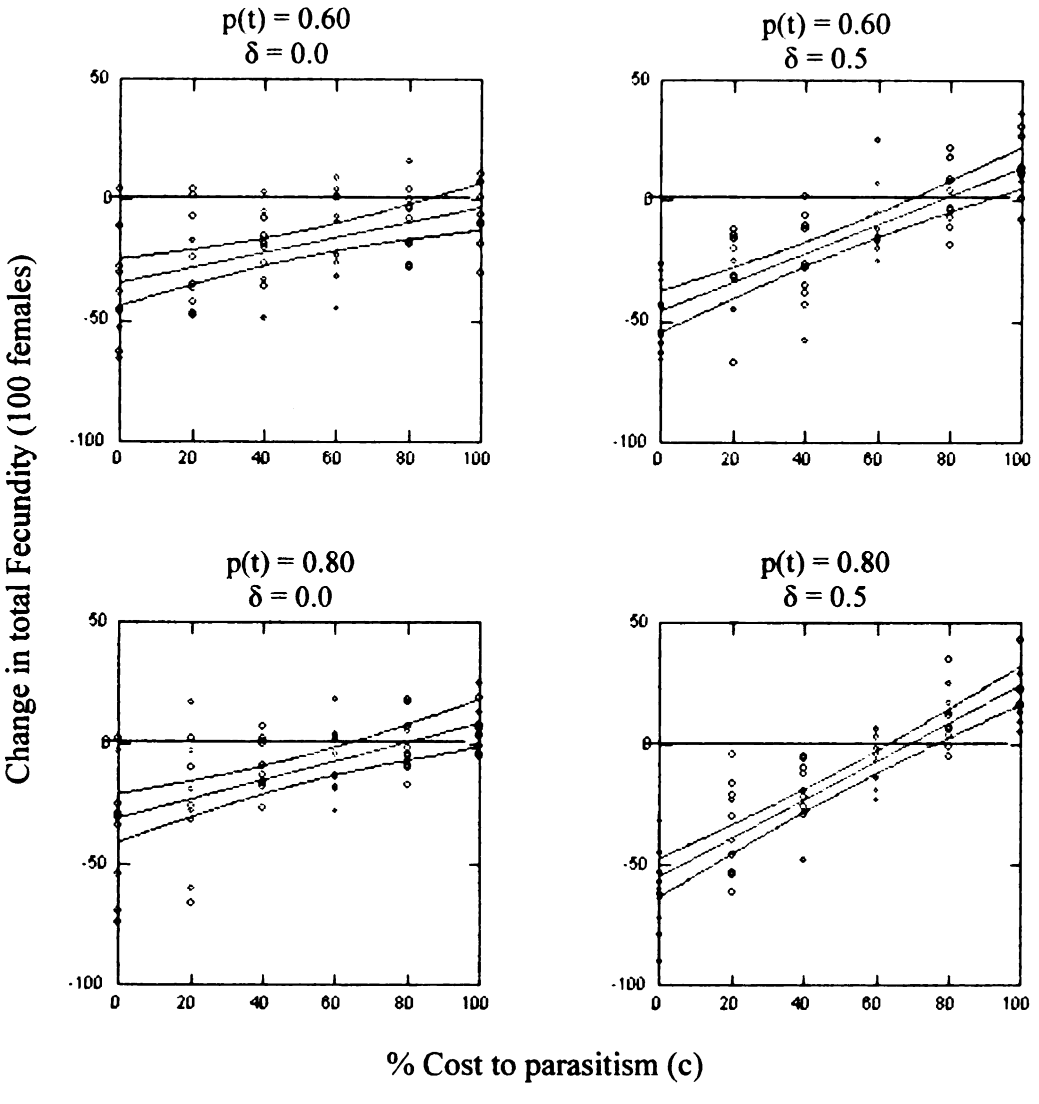


Figure 4-7. The relative change in total fecundity (between 0% and 30% predation) is positively related to the percent cost of parasitism (c). The point where regression lines (with 95% CI's) cross the x-axis denotes the level of cost to parasitism that must exist for a positive change in fecundity to occur. This point declines with increased parasitism rate, p(t) and differential predation (δ). See Table 2-7 for x-intercept values.

parasitism was set at 20, 40, 60, or 80% and each combination was simulated at five levels of cost to parasitism (c). The set resulted in 480 individual simulations for each combination of parasitism, predation, parasitism cost, and abandonment rate. All other parameters were held at standard conditions.

Several interesting results where apparent from these simulations. First, most abandonment frequencies only slightly affect the small positive change in fecundity when parasitism is high (Figure 4-8). Abandonment sharply influences the change in fecundity only when abandonment approaches 100%. Near this level, the positive change in fecundity due to predation disappears.

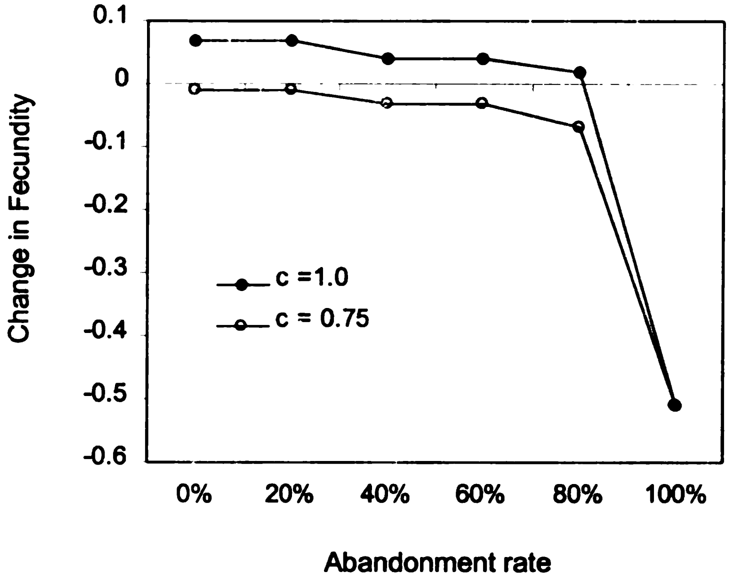


Figure 4-8. The mean change in fecundity (between 0% and 30% predation) at 80% parasitism is not strongly influenced by the abandonment rate except at very high abandonment. Results are given for two levels of cost to parasitism (c), and show that although the cost can influence the change in fecundity, this pattern is consistent with respect to the abandonment frequency.

The second result is that abandonment is not always profitable when parasitized (Figure 4-9). When there is a 50% cost to parasitism it does not pay to always abandon parasitized nests regardless of whether the frequency of parasitism is 40% or 80%. However, there is a clear advantage to always abandoning when the cost to parasitism is 75% and parasitism is 40% but not when parasitism is 80% (Figure 4-9). One would expect that as the cost and intensity of abandonment increased, the advantage of nest abandonment as a means to alleviate the effects of brood parasitism would increase. Modeling results contradict this conventional perception of the adaptive nature of nest abandonment. The reason for this contradiction is due to the probability of success for the subsequent re-nest following abandonment of a parasitized nest.

The specific threshold abandonment rate that will result in greater fecundity depends on three conditions: the cost to parasitism, and both the frequency of predation and parasitism. It pays to abandon a parasitized nest only if the subsequent re-nest has a higher probability of success. Thus abandonment is more likely to be profitable when the frequency of nest predation and parasitism are low and the cost to parasitism is high. Table 4-8 provides example threshold values of the cost of parasitism above which abandonment will increase seasonal fecundity.

Table 4-8. Approximate values of the cost of parasitism (c) necessary before an average female will gain in fecundity from abandoning a parasitized nest for 16 combinations of predation and parasitism rates.

	Predation (%)			
Parasitism (%)	10	30	50	70
20	0.23	0.34	0.46	0.62
40	0.30	0.41	0.54	0.68
60	0.40	0.51	0.63	0.76
80	0.55	0.65	0.75	0.85

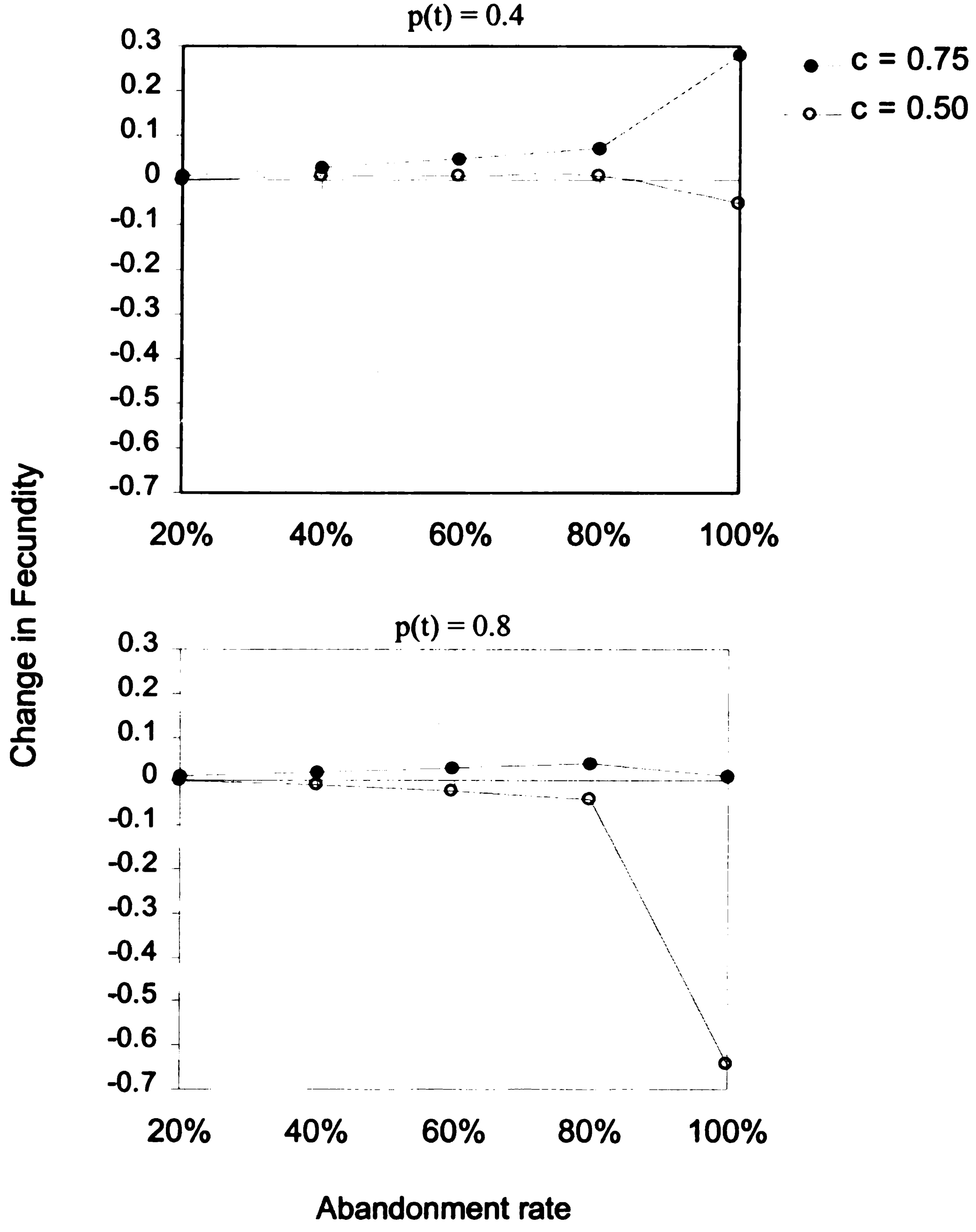


Figure 4-9. Nest abandonment positively changes fecundity relative to zero abandonment when the parasitism rate, p(t), is lower and the cost to parasitism, c, is higher, but has negative effects at high parasitism rates and/or lower costs to parasitism. These results are for 50% predation.

Numbers in Table 4-8 were estimated through minute manipulation of the value of c until fecundity was equal at zero and 100% abandonment. Below this value abandonment is not adaptive. For example, in a population with 50% predation and 40% parasitism it will pay to abandon an average parasitized nest only if the reduction in brood size (c) is greater than 54%. One important caveat is that that there is a range below this threshold value where intermediate frequencies of abandonment result in slight increases in fecundity such as seen for c = 0.50 at 40% parasitism in Figure 4-9. This is because at intermediate levels abandonment acts much like an increased predation rate for parasitized nests, allowing some birds to escape parasitism. Furthermore abandonment strongly affects changes in fecundity only at frequencies close to 100%.

Season length and Re-nest Frequency- Two final series of deterministic simulations explored the effect of re-nesting frequency on seasonal fecundity. One tested the length of the breeding season while the other tested the level of re-nesting frequency. To modify the length of the season the re-nest frequency was altered such that no more nest attempts were made after the given final day of the season. Five days prior to the last day r(t) was 1.0 (or all failed nests were replaced) and linearly declined to zero on the final day. Fecundity estimates were generated for four breeding season lengths at 20% intervals of predation and three levels of parasitism (Table 4-6). All other conditions were held at standard levels except that fifth nest attempts were allowed, with an average brood size equal to that of third attempts for all sites (Table 4-3). To accommodate the extended breeding season length, the total run time was extended from 100 days to 120 days to be sure that all nests were complete by the end of a simulation.

To test the level of re-nesting frequency, the initial value of r(t) was altered but the length of time when r(t) declines to zero remained similar to that seen in Figure 2-3. Four initial re-nest frequencies were tested: r(t) = 0.3, 0.5, 0.7, or 1.0. Exact values used for plotting r(t) in this second series are provided in Appendix A (Table A-3). Results were generated for four predation rates and two parasitism frequencies (Table 4-6). All other parameters were held at standard conditions.

Table 4-9 indicates that the change in mean young fledged between a 40 and 70 day season does not differ more than 0.03 young per female for all three parasitism rates. Therefore, the frequency of parasitism does not appear to influence the relationship between length of season and fecundity. This result is based on an abandonment rate of 0.10. Altering the abandonment rate does change the estimates of fecundity. However, the difference in fecundity did not vary from the pattern in Table 4-9 since increasing abandonment causes a slight increase in fecundity at both season lengths (data not shown). Also observed from this table is that the change in fecundity increases with greater predation frequencies, suggesting that the length of season is only important when nest predation is frequent.

Table 4-9. The change in mean young fledged per female between a season length of 40 and 70 days for three levels of parasitism.

	Predation %			
Parasitism %	20	40	60	80
0	0.05	0.21	0.40	0.44
40	0.06	0.21	0.39	0.41
80	0.05	0.21	0.38	0.41

The length of season also plays a small but notable role in whether intermediate nest predation can lead to positive changes in fecundity. A small positive change in fecundity occurs if the length of the season exceeds 50 and 62 days for 20% and 40% predation, respectively, for standard conditions at 80% parasitism (Figure 4-10). This plot suggests that even the impact of 60% predation on fecundity would approach zero at greater season lengths. In general, it appears that increasing the length of the breeding season reduces the negative effect of nest predation on seasonal fecundity.

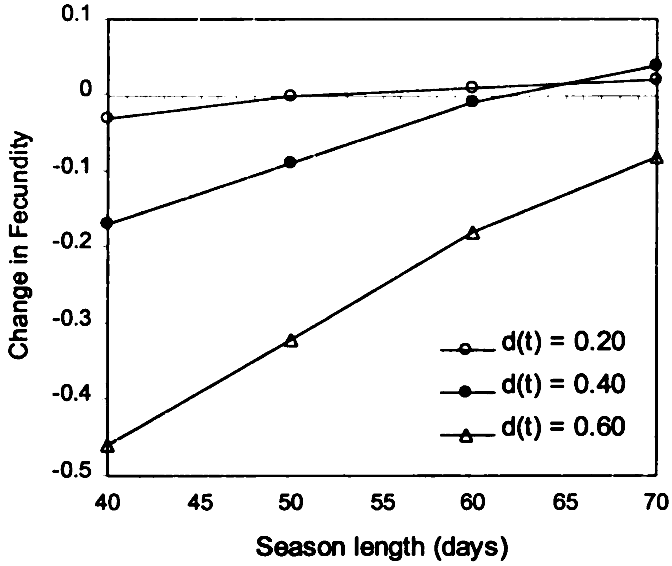


Figure 4-10. All else equal, increasing the length of the breeding season reduces the negative effect of nest predation, d(t), on the change in seasonal fecundity relative to zero predation. Results are for 80% parasitism.

The relationship between nest predation and seasonal fecundity shifts from a curvilinear to a linear pattern as the initial re-nest frequency declines (Figure 4-11). This pattern remains consistent at different parasitism levels. The effect of predation becomes increasingly more uniform across the entire frequency range when re-nesting becomes less frequent (Figure 4-11). Since the positive change in fecundity is a result of this

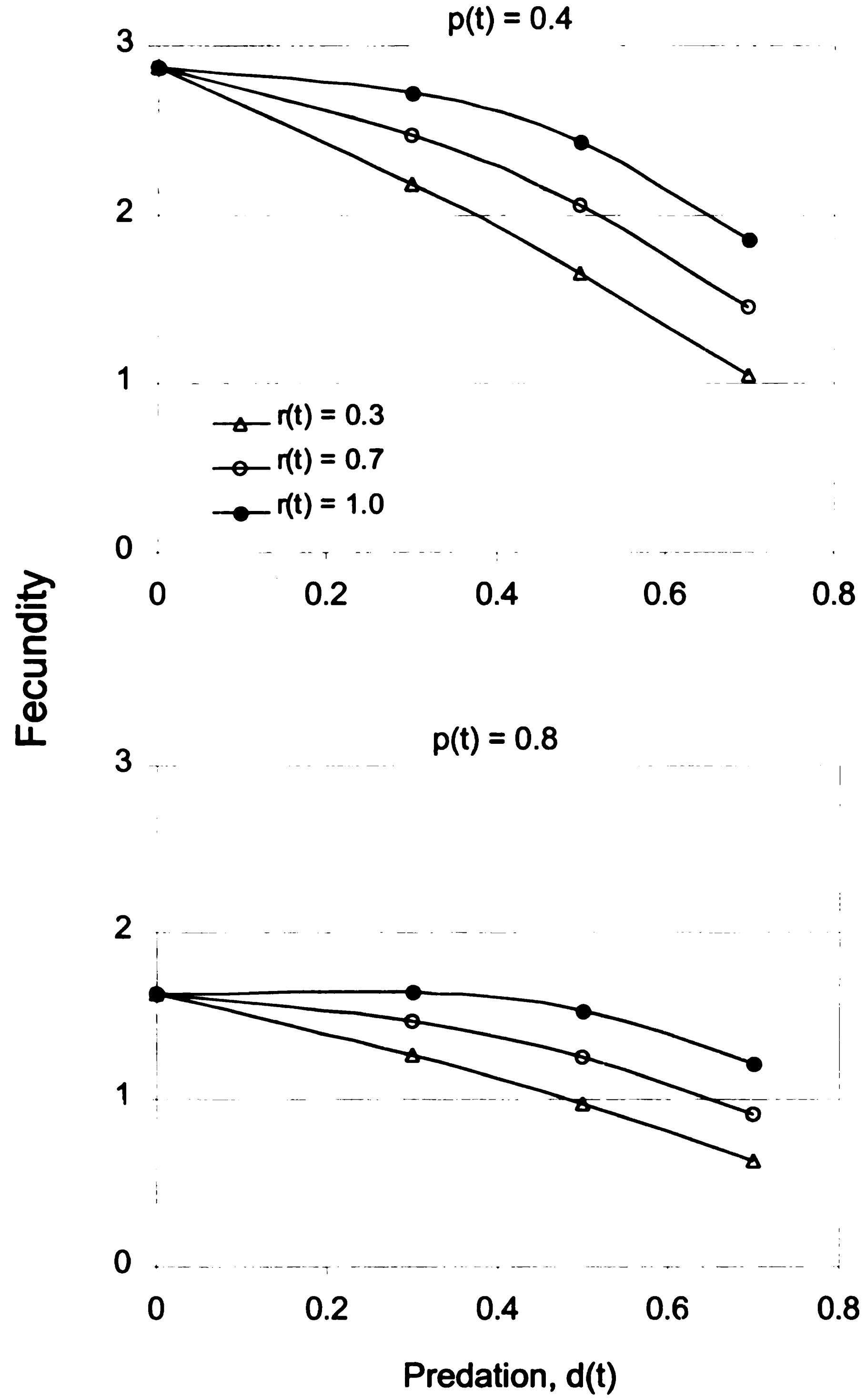


Figure 4-11. The relationship between nest predation and seasonal fecundity shifts from curvilinear to a linear decline as the initial re-nest frequency, r(t), declines. Results are shown for two levels of parasitism, p(t).

curvilinear pattern, at lower predation frequencies we expect that the potential for a positive effect to nest predation to dissipate quickly as the initial re-nest frequency drops. This is confirmed in Figure 4-12. The initial re-nesting frequency must be higher than r(t) = 0.967 in order for a population to gain from predation at d(t) = 0.3.

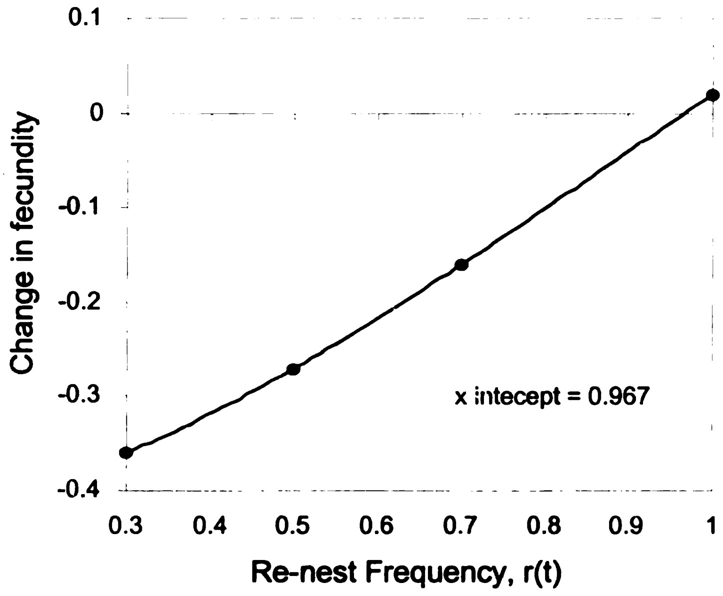


Figure 4-12. Any positive change in seasonal fecundity at 30% predation relative to zero predation quickly dissipates when the re-nest frequency declines. The x-intersection indicates the minimum initial level of r(t) necessary for a zero or positive change in fecundity to exist at d(t) = 0.3. A third-order polynomial was fitted to the data to generate the line from which the x-intersection was calculated.

Sensitivity analysis- It seems warranted to evaluate which of the above parameters have the greatest influence on seasonal fecundity. To do this requires the calculation of an index of the relative effect of each parameter on fecundity that is comparable for all parameters. This was done through the calculation of an elasticity index defined in the equation:

$$EI = \frac{\frac{f_2 - f_1}{f_1}}{\frac{n_2 - n_1}{n_1}}$$

Where, EI is the elasticity index, f_1 and f_2 are the two estimates of fecundity, and n_1 and n_2 are the corresponding values of the parameter for which elasticity is being calculated. The procedure is to run the model using the initial value of the parameter (n_1) and to find the estimate of fecundity (f_1). This is repeated for the second value (n_2) to find f_2. Therefore, the elasticity index is a measure of the relative change in fecundity relative to the change in the parameter in question. Parameters with higher magnitude EI values have a greater impact on the estimates of fecundity than those with lower values.

This analysis was performed on the following parameters, predation d(t), parasitism (declining) p(t), declining predation $d_d(t)$, cost to parasitism *c*, differential predation δ, abandonment *a*, and initial re-nest frequency r(t). All parameters are defined in the model as frequencies that can range from zero to one[1]. Also, as observed in previous results, most parameters vary in their relative impact on fecundity depending on their value. Therefore, elasticity of each parameter was calculated for three segments that divided the frequency range into thirds. The lower third was a comparison of the fecundity estimates for parameter values of 0.1 and 0.3, the middle third comparison was between 0.4 and 0.6, and the upper third was between 0.7 and 0.9. Most parameters also vary with respect to the level of predation and parasitism. Therefore EI values were calculated for *c*, δ, *a*, and r(t) for d(t) = 0.3, and 0.7 and p(t) = 0.4 and 0.8. EI values for predation (including declining predation) and parasitism were calculated at p(t) = 0.4 and

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[1] The exception is δ, which can include all real numbers, but realistically would range between 0 and 1 for most situations where parasitized nest failed more often.

0.8 and d(t) = 0.3 and 0.7, respectively.

Table 4-10 summarizes the top eight most influential parameters for each frequency range. Negative EI values indicate that increasing parameter values will decrease fecundity. As expected, the influence of a parameter generally increases with increasing frequencies of that parameter. In the lower and middle third frequencies ranges, results show that fecundity is most sensitive to the frequency of re-nesting and the effect of parasitism, both through the frequency p(t) and cost (c) Re-nest frequency is more influential at higher predation and parasitism. Fecundity is more sensitive to parasitism frequency at low predation rates and most sensitive to the cost of parasitism at high parasitism and lower predation rates. Both of these patterns show that predation can, under certain circumstances, reduce the overall impact of parasitism. Similarly, predation is more influential at low parasitism rates and is less influential when predation rates decline. Nest predation is the most influential parameter in the upper frequency range. Regardless, the influence of parasitism remains strong at high frequencies. Differential predation and abandonment were consistently the least influential parameters in predicting fecundity. This analysis supports the observation that fecundity is more limited by parasitism at low and intermediate frequencies, and is more limited by predation at high frequencies.

Discussion

Acting alone nest predation does not yield a positive change in fecundity under standard testing conditions. However, nest predation, in spite of lowering daily nest survival can increase fecundity when specific conditions are met. These conditions include parasitism

Table 4-10. The top eight most influential parameters according to frequency range. Parameter elasticity varied depending on the level of predation, d(t) and parasitism, p(t). Therefore, parameters are listed by specific levels for d(t) and p(t).

Frequency range					
Lower	EI	Middle	EI	Upper	EI
Re-nest Frequency, r(t) p(t) = 0.8 d(t) = 0.7	0.094	Cost to parasitism, c p(t) = 0.8 d(t) = 0.3	-0.448	Predation, d(t) p(t) = 0.4	-1.983
Cost to parasitism, c p(t) = 0.8 d(t) = 0.3	-0.077	Cost to parasitism, c p(t) = 0.8 d(t) = 0.7	-0.415	Predation, d(t) p(t) = 0.8	-1.944
Re-nest Frequency, r(t) p(t) = 0.4 d(t) = 0.7	0.076	Re-nest Frequency, r(t) p(t) = 0.8 d(t) = 0.7	0.406	Cost to parasitism, c p(t) = 0.8 d(t) = 0.3	-1.173
Parasitism, p(t) d(t) =0.3	-0.076	Parasitism, p(t) d(t) =0.3	-0.393	Cost to parasitism, c p(t) = 0.8 d(t) = 0.7	-1.056
Parasitism, p(t) d(t) = 0.7	-0.072	Parasitism, p(t) d(t) = 0.7	-0.356	Parasitism, p(t) d(t) =0.3	-0.990
Cost to parasitism, c p(t) = 0.8 d(t) = 0.7	-0.063	Predation, d(t) p(t) = 0.4	-0.335	Parasitism, p(t) d(t) = 0.7	-0.848
Cost to parasitism, c p(t) = 0.4 d(t) = 0.3	-0.038	Re-nest Frequency, r(t) p(t) = 0.4 d(t) = 0.7	0.333	Re-nest Frequency, r(t) p(t) = 0.8 d(t) = 0.7	0.731
Re-nest Frequency, r(t) p(t) = 0.8 d(t) = 0.3	0.038	Predation, d(t) p(t) = 0.8	-0.278	Declining predation, d(t) p(t) =0.4	-0.672

generally greater than 60%, a cost to parasitism greater than 75% reduction in brood size, greater predation on parasitized nests, and lower predation and parasitism for re-nests.

This positive change in fecundity is more likely to be observed when the breeding season is longer with a high frequency of re-nesting and when nest abandonment is infrequent. Most importantly, the positive change exists only when predation is generally lower than 40%. Not all of these conditions must be met simultaneously for a positive change in fecundity to exist. The two most essential conditions are frequent and costly parasitism. Given just these two conditions, a small non-significant positive change in fecundity can occur at or below 40% predation if the probability that a re-nest will be parasitized is lower (Figure 4-3). Other conditions only enhance this change and in some cases make it statistically significant (Figure 4-5).

A more striking result of these simulation experiments is that both parasitism and predation act in a complimentary way to reduce the effect of the other as each increases. This antagonistic effect is more evident for predation. There appears to be no change in fecundity for predation frequencies between zero and 30% when parasitism rates are approximate 70% or greater (Figure 4-2). The range of predation frequencies at which this occurs expands as the above conditions are met. Even predation frequencies as high as 70% can have little influence on fecundity (Figure 4-6).

Biological significance of findings- The positive effect of nest predation is not likely to be biologically significant in most situations since the change in fecundity tends to be relatively small. One exception is when that small positive change is sufficient to elevate productivity over the sustainability threshold. For example, if annual survival rates are

0.70 for adults and 0.35 for juveniles, a self-sustaining population with a 1:1 sex ratio would require 1.7 fledglings per female per year. For the conditions observed in Figure 4-6, fecundity increases from 1.63 to 1.78 young per female. Assuming the estimates of adult and juvenile survival are realistic, this small increase effectively switches the population from unsustainable productivity without immigration to a self-sustaining population. However, this conclusion is highly speculative because it is based on a number of assumptions and conditions being met and ignores possible difference in fledgling survival.

On the other hand, the effect of a reduced or no change in fecundity due to predation at high parasitism is likely to have significant biological consequences. This antagonistic relationship ultimate leads to weaker selection against both mortalities. Parasitism effectively reduces any selective pressure against nest predation if the overall frequency of predation is low. If cowbird abundance declines in the future, naturally higher predation may exist in the population due to the previous lack of selection to reduce predation of nests. Alternatively, nest predation, by reducing the impact of parasitism, has a similar effect of reducing selection for a host to evolve a defense against parasitism. This may contribute to the absence of cowbird rejection observed in many hosts despite severe costs to parasitism (Rothstein and Robinson 1994).

Current thought is that nest predation has the greatest impact on avian productivity (G&P, S&W, but see Woodworth 1999). While this may still hold true for many bird populations, this is clearly not the case for those populations suffering severe parasitism while only experiencing moderate predation rates. Since observed frequencies of predation in local populations are generally near 50% (Ricklefs 1969), we can expect parasitism when present and costly to be the limiting factor on productivity. Regardless, since the intensity of nest predation and parasitism is not fixed spatially or temporally, the relative impact of both will continually shift in populations. Moreover, results consistently show that both mortalities have a strong influence on seasonal fecundity. Therefore, proper management to recover an avian population must simultaneously reduce both nest predation and brood parasitism to effectively improve reproductive success. The best strategy to do so is to manage the habitat and landscape (Donovan et al. 1995a, Martin 1992a, Askins et al.1990).

Conditional simulations- Clearly, the interaction of nest predation and brood parasitism is influenced by an array of secondary conditions. Whether these conditions are likely to be observed in natural populations is of obvious concern. For example, as stated before most host species exhibit differences in level of cost to parasitism. Some, such as the Northern Cardinal can successfully raise a brood including a cowbird that is not significantly different in size to non-parasitized nests (Eckerle and Breitwich 1997). Other species like the Kirtland's Warbler (*Dendroica kirtlandii*) (Walkinshaw 1983), Prairie Warbler (Nolan 1978), or certain flycatchers (Sedgewick and Knopf 1988, Walkinshaw 1961) lose most or all young when parasitized. Therefore, the consequences brood parasitism will have on productivity will be species-specific.

The frequency of parasitism and predation are also highly variable in natural populations. Local frequencies for brood parasitism vary anywhere from zero to nearly 100% (Elliott 1978, Peck and James 1987, Robinson 1992, Robinson et al. 1995a and b). Frequencies of parasitism at or above 50% are a common occurrence for many cowbird hosts nesting in forest fragments and are typically highest along field-forest edges (Gates and Gysel 1978, Brittingham and Temple 1983, Robinson et al. 1995b, Donovan et al. 1995a). Every studied population of passerine experiences some level of nest predation. The frequency varies greatly depending on habitat, location, and an array of other conditions (Martin 1993a). Martin (1993b) has observed frequencies as high as 80%, but more commonly the frequency of predation ranges between 40 and 60% for open-cup nests (Ricklefs 1969).

Given this, a population with a high frequency of parasitism and moderately low predation may be common. However, east of the Rocky Mountains, the frequency of nest predation and parasitism are both positively correlated with habitat fragmentation (Gates and Gysel 1978, Wilcove 1985). In this region, one is more likely to find elevated nest predation in the same population that has high parasitism. Such a relationship is not conducive to the occurrence of a positive change in fecundity at intermediate levels of nest predation. Alternatively, current research on western populations suggests that predation and parasitism may be negatively correlated in naturally fragmented habitats common to this region (Tewksbury et al. 1998). Therefore, is seems plausible that high parasitism and low predation is likely to exist locally in some western regions. Finding those conditions that lead to a null or positive effect to predation in natural populations may prove challenging in eastern populations but perhaps less difficult in western populations. Ultimately, other auxiliary conditions must also have the potential to exist to increase the probability that this interaction does occur naturally. The following discussion addresses these specific secondary conditions.

Differential predation- How the overall frequency of nest predation is partitioned among nests seems to play a limited role in the consequences of nest predation and parasitism. While fecundity is relatively insensitive to this parameter, increased predation of parasitized nests does produce a positive change in fecundity that would not have existed if predation rates between nests were equal (Figure 4-5). As one might expect, if we increase predation on parasitized nests relative to non-parasitized nests we observe a gradual increase in seasonal fecundity (Figure 4-4). This is because predation is occurring on those nests that can benefit from nest failure.

The reverse trend, where increasing predation on parasitized nests results in depressed fecundity, is expected only at high rates of parasitism and predation. This occurred at 80% parasitism and 60% predation (Figure 4-4). Under these conditions, parasitized nests make a greater contribution to fecundity despite their low brood size because there are so few successful non-parasitized nests. Increasing the failure rate of parasitized nests at this point will naturally result in a decline in fecundity. For any given level of cost to parasitism, there is a threshold frequency for predation and parasitism, where greater predation on parasitized nests will no longer increase seasonal fecundity. As the cost to parasitism increases, this threshold will shift to higher frequencies. Therefore, for those species that are among the most concern due to parasitism (i.e. suffer severe consequences to parasitism) this reverse trend is not likely to occur often.

Are parasitized nests more likely to be depredated? Increased predation of parasitized nests exists in the mid-Michigan YWAR population (Figure 3-2). However, as discussed in Chapter 1, this pattern is not consistent in the literature and varies greatly from one study to another. In one classic study, parasitized nests of Song Sparrows failed more often (Nice 1937). On the other hand, a recent study of the Song Sparrow found

greater nest predation for non-parasitized nests (Arcese et al. 1996). Variation in the pattern of nest predation between nests is widespread, and suggests that whether parasitized nests are depredated more frequently depends on a variety of factors that may include the composition of the predator community, behavior of the local cowbird population, or habitat characteristics. Therefore, this condition is likely to exist locally but vary both spatially and temporally.

Declining predation- Greater nest success for re-nests means a reduction in the overall cost to predation. Since there is less cost from predation to overcome, it can be expected that this pattern would increase the likelihood of a positive effect to nest predation. Simulation results confirm this expectation. Slowly reducing predation to half its initial rate has one main result. The rate of decline (or slope) in fecundity as the initial predation rate increases is slower (Figure 4-6). This is also supported by the reduction in sensitivity of fecundity when predation declines (Table 4-10: upper range). Ultimately, this results in a wider frequency range where predation has no effect on fecundity.

Results from the YWAR study seem to suggest that lower nest predation for re-nests does not exist (Figure 3-3). According to model simulations, the cost of parasitism would need to exceed 80%, and there would need to be no change in nest predation between attempts before a detectible increase in fecundity would occur at intermediate nest predation rates in the studied YWAR population. If overall predation was half that measured in the field, or about 27 %, parasitism would need to exceed 90% for no effect of predation to exist across a broad range.

However, simulations found that no level of nest predation would lead to a positive change in fecundity, even at extraordinary high parasitism, when predation of re-nests compared to firsts nests are similar to that observed in the YWAR population. This is the case even when the cost to parasitism was 100%. It is clear from this observation that the success of re-nests is instrumental in the manifestation of a positive change in fecundity. Increased predation on re-nests appears consistent across years (Figure 3-3), suggesting an inherent causal mechanism within the population. Efforts to identify the reason for this pattern are the focus of the following chapter (Chapter 5).

Cost to parasitism- The success of parasitized nests is the central component of this system. Fecundity is strongly influenced by the cost of parasitism (Table 4-10). Ultimately, the effect brood parasitism has on seasonal fecundity depends on the impact raising a cowbird has on the host. If this impact is small then the cost of parasitism is small and nest predation will have similar costs for parasitized and non-parasitized nests. Results of these simulations show that the cost of parasitism must by high. In fact, if nests have a constant equal probability of failure then the cost must be nearly 80% of the initial brood size (Table 4-7). In other words, if a host can typically fledge 5 young when not parasitized, they must fledge only one young when parasitized before predation will increase fecundity for the entire population.

Though this cost seems high this is not uncommon. The Prairie Warbler population studied by Nolan (1978) would meet this condition, as would several other species including the Least Flycatcher (*Empidonax minimus*) (Briskie and Sealy 1987), Black-capped Vireo (*Vireo atricapillus*) (Gryzybowski et. al. 1986), Solitary Vireo (*Vireo solitarius*) (Marvil and Cruz 1989), Willow Flycatcher (*Empidonax traillii*) (Sedgewick and Knopf 1988, Walkinshaw 1961), and Bell's vireo (*Vireo bellii*) (Goldwasser et. al. 1980) (also see, Graham 1988). In fact, many populations suffer severe costs to parasitism, especially when multiple-parasitism is frequent (Robinson et al. 1995a). This threshold level of cost drops as other conditions are met such as increased predation on parasitized nests (Table 4-7). Therefore, the group of species for which this interaction could be relevant might be limited to those having high parasitism costs or populations where multiple-parasitism per nest is frequent, but certainly does not exclude all populations. In some cases, species of most concern, such as the Kirtland's Warbler, apparently experienced sharp population declines partly because of the costly effect of parasitism, making the interaction of predation and parasitism very relevant to their management. Current management practices do not explicitly take into account the potential importance of this interaction (see below).

Nest abandonment- It was initially expected that nest abandonment would eliminate the positive change in fecundity resulting from predation, since fewer parasitized nests would survive the abandonment stage to be exposed to predation that may benefit them. However, this was found not to be the case for most intermediate frequencies of abandonment (Figure 4-8). In fact, fecundity was not greatly influenced by abandonment rate. The reason for this is not entirely clear, but one reason may be that abandonment only occurs during a short window of time (during the egg-laying stage), while the time frame during which predation will occur includes this stage plus the much longer incubation and nestling stages.

Abandonment becomes effective only when sufficiently high so as to greatly reduce the number of parasitized nests that survive egg-laying. Beyond this point abandonment begins to have a much greater effect on estimates of fecundity. This threshold point lies greater than 80-90% abandonment under conditions simulated here.

Prior to reaching this threshold, abandonment has only a minor effect in reducing the benefit to predation as reflected by its consistently low sensitivity. Therefore, the fact that many populations of small songbirds show some level of abandonment (Rothstein 1975) will not eliminate them as candidates for observing a predation interaction. Only those species that show a very strong affinity to abandoning parasitized nests (rejectors) will never gain in fecundity at intermediate nest predation.

Another unexpected, and perhaps more interesting, result of the abandonment simulations is the conclusion that nest abandonment is not always an adaptive strategy to cope with brood parasitism. This directly contradicts results presented using Schmidt and Whalen's model (1999). They found abandonment was not necessarily adaptive for double-brooding songbirds but was always adaptive in single brooding populations. Nest abandonment is frequently cited in the literature as an adaptation to brood parasitism and is widespread in hosts (reviewed in Rothstein 1990). However, it is rarely an ubiquitous response to parasitism and for some populations is quite rare despite an apparently high potential for selection imposed by severe costs to parasitism (Rothstein 1990, Rothstein and Robinson 1994).

Several authors have pondered why hosts vary in their ability to discriminate and reject parasitic eggs (reviewed in Winfree 1999). Two general hypotheses, equilibrium and time lag, have been proposed to explain the maintenance of this variability. The time lag hypothesis suggests that abandonment or other forms of ejection have not become common because the population has not had sufficient time for genetic variants to appear and increase in the population (Rothstein 1990). As I have already stated, the antagonistic relationship between predation and parasitism may contribute to this lag time by reducing selectivity. The equilibrium hypothesis suggests that rejection can be non-adaptive if rejection incurs greater cost than acceptance. The most obvious cost to abandonment is the cost of losing young that would have fledged if the host accepted the parasitized nest. However, costs can also be measured by the potential for success of re-nests following abandonment. For example, in one host-parasite system, the parasitic bird is known to retaliate against those hosts that reject parasitized nests by depredating subsequent nests (Soler et al. 1999, Robert et al. 1999). Recognition errors where hosts abandon non-parasitized nests may also result in equilibrium (Rothstein 1982).

Results presented here suggest another plausible mechanism to support the equilibrium hypothesis. Abandonment is not adaptive when the frequency of predation and parasitism is high, even when the cost to parasitism is also high (Figure 4-8). Abandonment is not beneficial because the risk of failure for re-nests remains high. In order for nest abandonment to be adaptive, the potential reproductive success of the re-nest must be greater than that of the parasitized nest. As already stated, the frequency of parasitism and predation are both positively correlated with habitat fragmentation. Therefore, conditions where abandonment is likely to be non-adaptive can be expected to be common in fragmented habitats especially in localities east of the Rockies. However, the relationship between predation and parasitism is reversed in western populations (Tewksbury et al. 1998). Therefore, abandonment strategies will vary depending on region for those species with broad distributions. For these songbirds, mixing would lead to an overall equilibrium frequency to abandonment, while locally sharp differences in strategy may arise. Naturally, all this depends on the cost of parasitism. Abandonment will be adaptive if the cost to parasitism is sufficiently high as to incur a greater cost than the lower reproductive success rate of re-nests.

Season length and re-nesting frequency- Nest predation has less of an impact on fecundity in a longer breeding season (Figure 4-10). This result is consistent with others (Grzybowski and Pease, in press). If a songbird has more opportunities to nest following failure a re-nest is eventually likely to succeed. Longer breeding seasons provide more opportunity for re-nests to ameliorate the negative effect of nest predation. However, the relative contribution of length of the season on seasonal fecundity is not large. A more than 40% increase in the length of the season increases fecundity per female by 0.41-0.44 young (Table 4-9). Also, if we were to extend the breeding season of the YWAR population by 20 days, through appropriately adjusting the observed re-nest frequency (Figure 2-3), the resulting increase in fecundity would be between 0.11- 0.22 young per female for the range of predation observed in the field. These are small changes in fecundity relative to those resulting from equivalent percent changes in nest predation and brood parasitism. Season length is likely to play a greater role in seasonal fecundity in multiple brooding species, since those that were successful will have more opportunity to start second broods.

Alternatively, seasonal fecundity is clearly very sensitive to the frequency at which failed attempts are replaced (Table 4-10). The likelihood that a nest will eventually succeed is greater when failed nests are replaced more frequently. Moreover, higher re-nesting frequencies increase the curvilinear relationship between predation and fecundity (Figure 4-11). Grzybowski and Pease (in press) found a similar result and suggest that this curvilinear relationship is because increasing predation does not produce proportionate decreases in seasonal fecundity. The reason being that when predation is more frequent it occurs, on average, earlier in the nesting cycle thereby utilizing less of the breeding season. Therefore, more re-nest attempts can be made. Increasing the frequency of re-nesting amplifies this relationship. A high frequency of re-nesting seems to be an adaptation to ameliorate the negative effects of nest predation.

An obvious question is if re-nesting can reduce the effect of predation why do birds eventually stop re-nesting? The answer involves additional long-term costs to re-nesting. The survival of fledglings from re-nests may be lower if food supply diminishes in the latter part of the breeding season. These young also have less time to prepare for the southern migration and thus may have lower over-wintering survival compared to fledglings from original nests. Moreover, there is a well-recognized trade off between fecundity and survival (Williams 1966, Linden and Moller 1989). In general, greater fecundity comes at the cost of lower adult survival. This relationship should lead to an optimal breeding season length that limits the number of nest attempts. Birds must also cope with other necessary stages of their annual cycle such as the need to molt feathers and/or prepare for long migrations. Extending the breeding season would shorten or eliminate the time necessary for these activities.

Comparison with existing models- FLEDGE differs in several ways from two similar existing models (Table 4-11). Both existing models are superior to FLEDGE in that they can model species that fledge more than one brood in a season. On the other hand, FLEDGE has notable advantages over these nesting models. The most striking is that FLEDGE does not assume that brood size for all nest attempts remains constant. This assumption is inconsistent with Nolan's (1978) data and the YWAR data (Table 4-3). It

Table 4-11. Key comparisons of parameterization and assumptions between three existing models for predicting seasonal fecundity.

Condition	FLEDGE	Pease & Grzybowski[a]	Schmidt & Whelan
Predation rate	Variable. Defined by plotting frequency curves versus time.	Variable Define in mathematical functions	Constant
Parasitism rate	Variable. Defined by plotting a frequency curve versus time.	Variable: Define in mathematical functions	Constant Defined as proportion
Cost to parasitism	Constant for all nests	Constant for all nests but can adjust for multiple parasitism.	Constant for all nests
Clutch reduction	Variable brood size per attempt	Constant brood size for all attempts	Constant brood size for all attempts
Abandonment	Constant rate. Will abandon last attempt.	Temporally constant but value can vary depending on degree of parasitism. Will abandon last attempt	Constant but will not abandon last attempt.
Re-nesting	Limits number of re-nest Limits season length Defined as frequency plotted versus time	Limits length of season- but unlimited attempts. Variable frequency defined in mathematic function.	Limits number of attempts Constant frequency
Double brood	No	Yes	Yes
Multiple parasitism	Not explicitly modeled	Can adjust brood size according to number of cowbird eggs present	Not explicitly modeled

a. Comparisons were made with the more generalized model offered by P&G. Their simpler models have greater restrictions.

also differs from both in how it models re-nesting behavior. Pease and Grzybowski (1995) allow re-nesting to occur for a fixed length of time, while Schmidt and Whelan (1999) limit the number of re-nests a bird will attempt. Using FLEDGE, the number of re-nests a female can make and the length of time during which re-nests will be made are both incorporated into the probability of re-nesting. Furthermore, unlike the S&W model, FLEDGE does not assume predation and parasitism rates must be constant. Finally, FLEDGE takes advantage of STELLA's® graphical input devices to greatly simplify data entry, manipulation, and mathematics (Constanza et al. 1998). Parameter values can be defined with the click of a mouse and many different simulations can be performed in a matter of minutes. Neither of the other models has this feature.

While the P&G model is superior in ability to model a broad set of situations, this advantage is at the cost of simplicity, thus limiting those who can quickly understand and utilize it. Furthermore, Pease and Grzybowski (1995) freely admit that there are rarely sufficient data available to parameterize their general model, noting that even Nolan's (1978) outstanding data set is inadequate. To rectify this problem, they propose a simpler model that assumes constant predation and parasitism, and assumes that the number of young that fledge from parasitized nests is constant regardless of number of cowbird eggs laid, among other restrictions. FLEDGE inherently does not require any assumption about the variability of nest predation and parasitism with regards to time, and all necessary data to parameterize the model for the YWAR were attained from existing data and from a low cost four year study. Thus FLEDGE offers a compromise between the overly simple S&W model and complexity of the P&G model.

Both Schmidt and Whelan (1999) and Grzybowski and Pease (in press) have used their models to evaluate the relative effect of predation and parasitism on seasonal fecundity. In S&W's analysis, they concluded that nest predation has a greater impact on fecundity than parasitism. This conclusion seems contrary to the findings presented here which suggest that fecundity is more sensitive to parasitism over a larger range of frequencies. However, my simulations examined a slightly different set of conditions than that of S&W. Most notably, my simulations dealt with birds that suffer at least 75% reduction in fecundity when parasitized. Although less apparent, a similar pattern of increased fecundity within a limited range of nest predation exists in S&W's results when the cost of parasitism was severe. They also found that the effect of nest predation was diminished when brood loss was large in parasitized nests as shown by the vertical lines of the isopleths (Schmidt and Whelan 1999: figure 2). They conclude that nest predation is more important because the range at which this occurs is small.

Grzybowski and Pease (in press) also conclude that predation generally influences seasonal fecundity to a greater degree than parasitism, but they are quick to point out that parasitism becomes increasingly more important as the cost of parasitism increases. Their analysis did not explore the possibility of a benefit to nest predation. However, all three models consistently found that the effect of predation is reduced with increasing parasitism. Perhaps the main reason why predation is more important for a greater range of parameter space in S&W and P&G's results lies in the most significant difference between these models and FLEDGE. Both of these models presented results for double-brooding songbirds. Since second broods occur later in the season when parasitism is likely to be infrequent, nest predation incurs the greatest cost on these nests. Moreover, re-nesting contributes an additional cost to multiple-brooding birds in that it shortens time available to attempt second broods. This likely results in a finding that predation is more influential. This is supported by S&W's results for single-brood populations, where parasitism makes a greater contribution to fecundity.

Variation in our conclusions is reflective of the importance of knowing the conditions that exist in the population of concern. Which factor is more limiting will depend not only on the frequencies observed in the population but also an array of other conditions and life-history characteristics. As Grzybowski and Pease (in press) point out, the complexity of the interaction between brood parasitism and nest predation greatly complicates the interpretability of nesting data alone. All available information needs to be considered when trying to assess the factors influencing population growth in songbirds. The influence of brood parasitism and the resulting interaction with nest predation is dependent upon the performance of the host when parasitized as well as the female's ability to successfully re-nest following failure from nest predation. The interactive effects of nest predation and brood parasitism will be species-specific and no generalized conclusions for all species can be convincingly made. For example, Woodworth (1999), using the model introduced by Pease and Grzybowski (1995), found brood parasitism to be more important than predation to population viability for a tropical endemic songbird.

Conclusions and Implications for Management and Research. - Results presented here suggest that when brood parasitism exists and the cost to the host is sufficiently high, seasonal fecundity is influenced more by brood parasitism than nest predation in single-brooding songbirds. Moreover, moderate to low predation rates have little or no detrimental effect on fecundity in populations experiencing frequent and costly parasitism. These results support Brittingham and Temple's (1983) conclusion that brood parasitism and not nest predation is a leading cause in the decline of several species in temperate North America.

Efforts should be made to minimize cowbird abundance in managed populations. Combined with habitat management, this approach has proven effective in the past in some populations (Walkinshaw 1983). However, this is not always the case (Robinson et al. 1993). Stutchbury (1997) found cowbird removal to have no detectible effect on fecundity of the Hooded Warbler despite dramatically decreasing the parasitism rate on nests. Modeling results presented here or by others (Schmidt and Whelan 1999, Grzybowski and Pease, in press) help to explain why the same management strategy can give such divergent results. As one mortality factor is reduced, the other becomes more limiting on seasonal fecundity. Moreover, seasonal fecundity becomes more sensitive to nest predation when it exceeds 60% no matter what the level of parasitism. These are results shared by all models.

Therefore, to reiterate the conclusion by others, the best approach to promoting population growth is to reduce both causes of mortality. This is best accomplished by preserving larger tracts of high quality breeding habitat (Martin 1992a, Donovan et al. 1995a). When this is not a reasonable strategy, the use of models such as FLEDGE or P&G can evaluate which management options will result in the greatest increase in seasonal fecundity (for example see Liu et al. 1995).

Several questions remain unanswered that have direct implications for the observed interaction between nest predation and brood parasitism. FLEDGE was not designed to address lifetime fecundity, thus it is not clear what cost nest predation has over the lifetime of a host. Although re-nesting may improve short-term seasonal fecundity, it is plausible that there is a greater cost in lifetime fecundity (Linden and Moller 1989). For example, some young that fledge later in the season have been shown to have lower over-winter survival (Lack 1954, Williams, 1966). Lower survival of young from re-nests may cancel out any increase in fecundity due to nest predation. However, there may be additional unaccounted costs to raising a cowbird as a result of the extra effort parents must make to feed the young. Parasitism may shorten an adult's lifespan and host young that fledge may have lower post-fledgling survival compared to young fledged from non-parasitized nests. As discussed, differences in nest survival between parasitized and non-parasitized nests also remain unclear. Furthermore, I found few studies that clearly identify the probability of re-nesting following nest failure and how this changes as the season progresses (but see, Rooneem and Robertson 1997). To better understand the impact of nest predation and parasitism on real populations, more data are necessary on the frequency and consequences of re-nesting.

CHAPTER 5- ARTIFICIAL NEST EXPERIMENT

The frequency and success of re-nests can influence the outcome of predation-parasitism interactions. As noted in Chapter 4, model simulations suggest that no level of cost or frequency of parasitism will result in a positive change in fecundity at intermediate predation, if re-nests have lower nest success. While YWAR do re-nest frequently these re-nests are not as successful as first nest attempts (Figure 3-3). Even so re-nests make a significant contribution to seasonal fecundity and thus are important to sustain a population (Table 3-2). Therefore, identifying the mechanism(s) causing the observed increased failure for re-nest was of great interest. Understanding the mechanisms and differences by which re-nests survive could provide insight into management of certain avian populations and could provide insight into the evolution of nest site specificity.

Several hypotheses can explain the pattern of reduced success of re-nest attempts. These can be divided into two general themes: those concerned with variation within or between individual birds (Individual-based hypotheses) and those concerned with variation in external factors beyond the influence of the breeding adults, such as attributes of nest predators. These are not necessarily mutually exclusive since adult behavior can be modified by external factors, and the actions and choices of individual birds may influence some external factors, namely predator activity. These hypotheses are summarized below and in Table 5-1.

Individual based hypotheses- A re-nest occurs because a prior nest attempt failed. Attributes associated with nesting adults may very well increase the likelihood of failure. It would seem then that these very same attributes would reduce success for any

Table 5-1. A summary of hypotheses to explain the greater nest predation rate on re-nests including the aspects of the study used to evaluate them, and predictions if supported.

Main Hypothesis	Alternates	Experimental design or measured variables	Prediction if supported
Individual based hypotheses:	Poor parental quality: Parental behavior	Behavioral measurements	Parental behavior differs between successful and unsuccessful individuals.
		Dummy vs. active nest success	Dummy nests have greater nest success.
	Poor parental quality: Territory quality	Vegetation measurements	Attributes of surrounding vegetation differ between successful and unsuccessful individuals.
		Dummy vs. active nests	Dummy nests have lower nest success on territories of less successful active nests.
	Nest placement hypothesis	Vegetation measurements	Pair-wise comparisons of nest attempts will vary in vegetation composition.
Predator-based hypotheses:	Predator return behavior	Timing of predation events	Predation events of paired active and dummy nests would occur close to each other in time.
	Predator peak activity	Frequency of nest predation versus time for active and dummy nests.	Temporal variation in nest predation frequency exists in data.
	Nest density dependence	Nest predation rate versus number of exposed nests.	Periods of highest predation occur during highest nest density- predators show density-dependent response.

subsequent nest attempt. Consequently, re-nests show greater failure because they are composed of a greater proportion of nests by these inferior breeding adults. Thus the first hypothesis, which I will call the poor parental quality hypothesis, states: Re-nests, which include only those birds that have already failed, are inherently composed of inferior birds with a lower potential for nest success. The main assumption of this hypothesis is that those qualities that contribute to lower nest success in some individuals do not vary within a season. For example, birds do not "learn" from previous failure. Two main qualities of breeding adults are plausible attributes related to nest success: parental behavior and quality of the defended territory. These are not necessarily mutually exclusive since adult behavior affects selection and defense of territories.

Parental behavior has been documented as a factor in nest success. The frequency of visits made to the nest (Martin 1992b), their age and hence experience (Saether 1990), or how they behave in the presence of potential predators (McClean et al. 1986, Cresswell 1997, Hatch 1997) are linked to nest success. Other attributes associated with behavior such as nest placement and how well they conceal the nest, or how elusively they approach their nest, can also contribute to nest success. In addition to parental behavior, characteristics of the territory such as the diversity of vegetation structure (Martin 1988a, Marzluff 1988) or the abundance of snags (Anderson and Storer) are also known to influence nest success. Moreover, territories with large shrub patches may contain more potential nest sites for a visually searching predator to investigate thus reducing the risk of a single nest becoming discovered (Martin and Roper 1988). All these attributes are likely to vary between individuals (Martin 1986) and thus all nest attempts by one individual will have a different probability of success than those of another individual.

An alternative individual-based hypothesis states that sub-optimal nest placement of re-nests caused their lower nest success (nest-placement hypothesis). It is likely that natural selection has acted to have birds choose nest locations that have the greatest potential to minimize discovery by predators (Martin 1988b). YWAR have been shown to select nest sites based on characteristics of the nest patch, preferring horizontally larger shrub patches (Knopf and Sedgwick 1992). Thus it seems plausible that first nests are placed at a location within the territory that maximizes the chance of success. Subsequent re-nests are less successfully because the better nest sites were already used.

For example, female YWAR may place her first nest in the largest patch of meadowsweet or rose that is furthest away from snags. However, if by chance this nest fails, it is unlikely that she will re-nest near this location (pers obs.). In fact, those studies that have examined future nest placement have found that re-nests following predation tend to be placed spatially distant from the previous nest (Harvey et al. 1979, Marzluff 1988, Howlett and Stutchbury 1997). This may occur because, once a nest is found, predators might re-visit the general area around the nest (Martin 1992a, Sonerund and Fjeld 1987). Thus a re-nest placed in the same general area would have a greater risk of becoming discovered. A bird may sacrifice quality of nest site by placing the re-nest in a more remote location from the original nest. Because of the behavior of predators, the re-nest has a better probability of success than a second nest placed in the higher quality nest site. Abundance and dispersion of suitable nest patches within a territory will contribute to this. For example, a greater discrepancy in nest success might be observed between first nests and re-nests if preferred nest plant patches are small or few and far between, leaving re-nests to be placed in distinctly less suitable sites. Thus habitat and territory quality are likely linked to this hypothesis as well.

Predator behavior based hypotheses- One alternative to individual based hypotheses states that temporal changes in predator behavior or abundance results in increased nest predation for re-nests. As state above, some predators may re-visit previously discovered nest sites (Sonerund and Fjeld 1987). All else being equal, this behavior would seemingly increase the probability of failure for subsequent nest attempts within the general area of the previous nest (the predator return hypothesis). It is also plausible that predator nest searching behavior varies temporally and that re-nests occupy a greater proportion of the total available nests during the peak foraging rate of dominate nest predators (Peak activity hypothesis). Moreover, some predator communities show density dependent nest predation (Martin 1993 a and b). A greater proportion of all available nests (including other species) may be re-nests during the period of highest active nest density (density-dependent hypothesis).

According to foraging theory most vertebrate predators that actively search for specific prey should show density dependence (Martin 1993a). As the number of nests in a given area of all similar species increases, predators learn to associate a reward with bird activity. Therefore we would expect to observe a relationship between nest predation and the number of active nests if nest predators are actively searching out nests. YWAR arrive and begin breeding earlier than many other migrants. Therefore, initial nest attempts may be made during a period of lower nest density. It is also plausible that some nest predators simply increase their intensity of foraging on nests later in the season when more replacement nests are active. For example, circumstantial evidence suggests that Blue Jays are a common nest predator. These birds begin breeding earlier in the season than most Neo-tropical migrants (Brewer et al. 1991). The stage when most Blue Jay nests are fledging and young jays are foraging for the first time may overlap with the period of time when re-nests dominate the pool of active nests.

In this chapter I describe and present results from a field experiment designed to aid in discriminating between these alternate hypotheses. Since most of these hypotheses are not mutually exclusive, a myriad of secondary measures were collected to support or refute certain hypotheses noted above. These include both behavioral assessments and territory quality assessments as described in Chapters 2 and 3. Many of these comparisons have been presented in Chapter 3 but more specific contrasts, as described in Table 5-1, are presented below.

Experimental design- Previously used nests of YWAR and American Goldfinches (*Carduelis tristis*) (which have similar nests) were collected during the non-breeding season for use as dummy nests (USFWS collection permit MB008925-0). During the breeding seasons of 1999 and 2000, active nesting territories were randomly selected and a dummy nest, with at least two infertile Zebra finch eggs as bait, was placed in a random location within these territories. Territory boundaries were determined through male activity. Active nesting territories had a nest with at least one egg and frequent adult activity determined from nest monitoring.

Dummy nests were placed in locations with qualitatively similar vegetation and concealment as active nests and were not placed closer than 5 meters from active nests. For example, if the active nest was placed in meadowsweet I tried to place the dummy nest in another meadowsweet patch within the territory. If no other suitable meadowsweet patches were available I selected another preferred nest plant such as gray dogwood or rose depending on availability. In this manner, all factors that may influence nest success were controlled except for the influence of parental activity. Dummy and natural nests were monitored every 2 to 4 days for signs of predation. If an active nest was depredated and a re-nest was built, the dummy nest was relocated to a new site within the territory. Dummy nests were not replaced if depredated unless the active nest also became depredated and a re-nest followed. Before a dummy nest was removed the tape distance, side concealment, and overhead cover were recorded. The latter two measures were not recorded during 1999.

In addition to the Zebra Finch eggs, one or two clay eggs shaped and painted to resemble YWAR eggs were added to dummy nests. Since actual predators consuming nests can differ from those observed to be present (Fenski-Crawford and Niemi 1997), nest damage (Best and Stauffer 1980) and markings on clay eggs were used to identify predators (Haskell 1995). The following criteria were used to classify nest predators. If the clay eggs remained, I examined them for any markings and indentations. Tooth marks indicated a mammalian predator. I also classified a predator as mammalian if the nest was dislodged from the support branches or torn or if fresh tracks were observed nearby. I assumed avian predators if markings on clay eggs suggest the edges of a bill or puncture by a bill or if all eggs were missing with no damage to the nest. I assumed snake predation if only the zebra finch eggs were missing and no markings were observed on the clay eggs. Based on these criteria, I determined that 50% (n =13) of dummy nests were depredated by birds, 35% (n = 9) by mammals, and 15% (n = 4) by snakes.

Artificial nests are commonly used in studies of avian nest predation but have some inherent problems associated with them (Wilson et al. 1998). This experiment includes several modifications from traditional artificial nest studies to reduce these problems. First, artificial nests were actually previous-year or in some cases earlier nest attempts of YWAR. Some goldfinch nests were also used simply because they were often difficult to distinguish from YWAR nests during off-season collection. Using the same or very similar nests will eliminate any bias in predation resulting from the size, shape or color of the nest that may influence detection. One potential problem is that the scent of these nests differed. Goldfinches will defecate on the rim of nests (Watt and Dimberio 1990). Although visual evidence of this was absent in weathered nests, goldfinch nests may be more detectable than other nests. However, these nests represented only a small proportion of those collected since goldfinches were far less abundant on the sites. Thus any affect this might have was likely small.

An additional improvement from traditional artificial nest studies was the use of zebra finch eggs, the dimensions of which closely match those of YWAR eggs. Consequently, potential predators that may be able to consume one egg size and not another are not excluded from either set of nests (Haskell 1995, Lindell 2000). Many artificial nest experiments also place dummy nests on the ground. However, some studies reveal differences in nest predation between ground nests and elevated nests (reviewed in Martin 1992a). In an attempt to match all conditions of nest placement with that of real nests, I placed dummy nests in elevated positions in preferred nest plants (Table 4-5). Dummy nests were sewn in to branches using a needle and dark thread, in order to secure nests into the shrubs. Lastly, dummy and active nests were monitored simultaneously for direct comparisons.

Zebra finch eggs were provided by the avian research lab on the campus of Michigan State University supervised by Dr. Juli Wade. The supply of eggs proved to be the limiting factor in sample size. Dr. Wade's lab supplied about 100 eggs in each season. With the inevitable breakage of some eggs during placement, only about 40 artificial nests were used in each year.

By comparing nest predation rates of natural versus dummy nests, I was able to determine which factors seem likely to influence nest success. For example, greater nest predation on natural nests would suggest that parental activity influenced a predator's ability to locate them. If this pattern persisted for additional nest attempts, one could conclude that certain birds have poor nesting skills. Increased predation of dummy nests that are on territories of less successful birds would suggest that poor territory quality affects seasonal nesting success. Finally, any temporal change in intensity of nest predation on dummy nests could reveal the impact of changes in predator foraging rate during the breeding season. Specific predictions from experimentation and data collected are outlined in Table 5-1.

Results- Overall nest predation rates did not differ significantly between dummy and active nests (Figure 5-1). Parental behavior was associated with nest fate during nest construction but the relationship was weak and practically absent when corrected for experiment-wise error (Table 3-10). These results indicate that adult behavior at the nest did not influence the probability that a predator would discover a nest. However, dummy nests on territories for which the active nest also was depredated had a much greater failure rate (Figure 5-2). This result supports the poor parental quality hypothesis. Given that dummy nests lacked parental activity it seems likely that characteristics of the occupied territory that both the active and dummy nest shared caused greater nest failure. This could have been specific nest placement or overall territory quality.

Alternatively, it is also possible that greater predation on dummy nests in some territories was caused by predator behavior. If predators do in fact return to the location of a previously discovered nest, other nests in that immediate area would seemingly have a greater chance of becoming discovered. Unfortunately, this experimental design cannot discriminate this from the effect of territory quality. To do so would have necessitated simulated nest predation by humans and testing for differences in nest success between re-nests following human predation and natural predation events. I elected not to increase predation artificially to avoid undue mortality in the population.

For those territories in which nest predation occurred on both the active nest and dummy nest, the mean number of days between predation of each nest was four. No indication of skew in the data existed. Of the 20 nests for which this occurred, the distribution was almost evenly divided by the mean. Predation events occurred less than 4 days apart in ten cases and eight occurred more than 4 days apart. This relatively uniform distribution suggests that nest predation was random. This is likely biased toward a lower mean time period since many dummy nests were removed within a week after active nests were destroyed in order to accommodate a re-nest attempt. If predators do return to the location of a previously discovered nest, it is not known for how long of a time interval. One would assume that they would do so most frequently during the same day. A greater time interval between predation events leads to a greater likelihood that

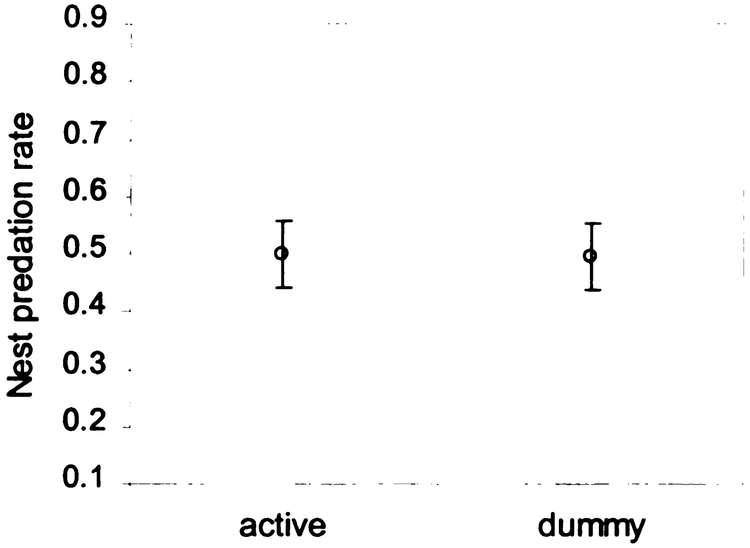

Figure 5-1. Mayfield estimates of overall nest predation were nearly identical between paired dummy and active nests (n = 81) ($X^2 = 0.0032$, $p = 0.96$). Error bars denote standard error.

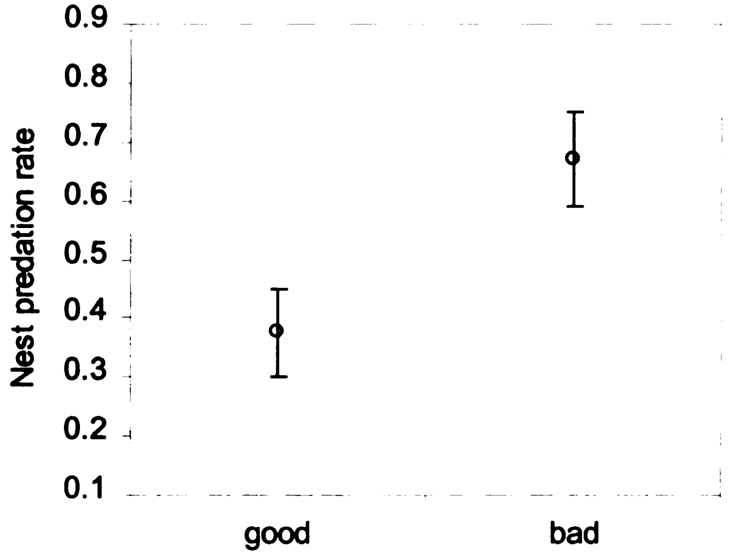

Figure 5-2. Dummy nests on territories of successful active nests (good, n = 42) had significantly lower predation than dummy nests on territories of active nests that failed (bad, n = 39).

each event was independent. An average of four days between predation events appears sufficiently long enough to suggest the predation events were independent. However, there is no way of knowing this for certain with the data available.

There is no evidence to suggest that abundance or frequency of nest predation varies within the season. A comparison of predation rates on dummy nests placed during the first half of the season to those placed during the second half of the season found no difference (Figure 5-3). There is also no evidence to suggest that nest predation rates fluctuate with nest abundance (Figure 5-4). These results suggest that increased predator activity or density dependent predation does not exist in this habitat and thus cannot explain the greater predation on re-nests. While in the field, no noticeable temporal change in abundance of suspected predators such as Blue Jays or crows were detected. I regret not making point count and scent station surveys of potential predators during the season, but time and human resources available were limited.

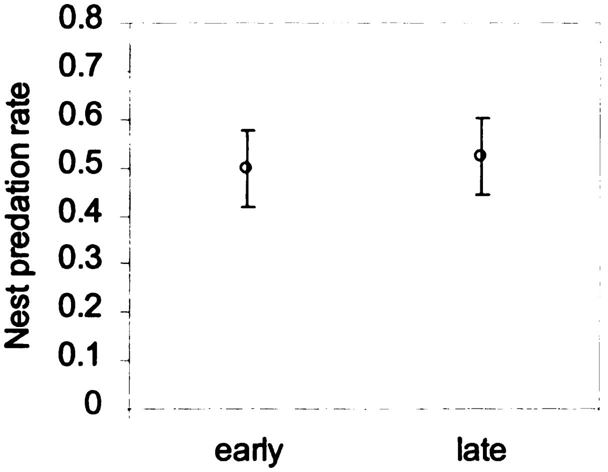

Figure 5-3. Nest predation rates of dummy nests introduced in the first 25 days (early) did not differ from dummy nests introduced in the latter half of the season.

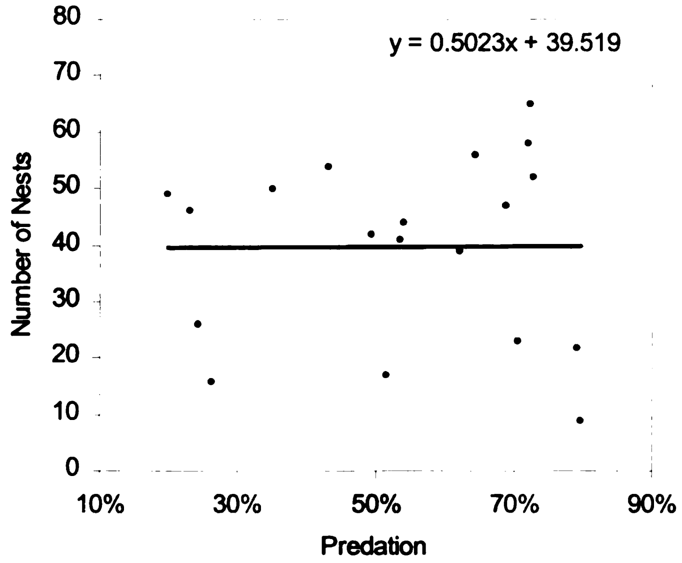

Figure 5-4. A linear regression analysis found no significant increase in nest predation in relation to nest abundance. Points represent the predation rate for a single site by week (years pooled). The linear regression line and equation are included.

Like active nests, nest concealment of dummy nests influenced nest success. An ANOVA found depredated dummy nest had significantly longer tape distances (Table 5-2). Side cover was not significantly different between successful and depredated dummy nests, but mean side cover of depredated nests was lower (Table 5-2). Similarities with active nest concealment indicate that predators do seem to be opportunistic (especially avian predators). In other words, predators do not appear to actively search out nests but depredate nests when accidentally discovered.

Tape distance can be an indicator of territory quality. Dummy nests on territories of depredated active nests had significantly longer tape distances than those on successful territories (F = 4.345, df = 81, p = 0.040). Dogwood species tend to be less dense with respect to branches and foliage and thus do not obscure nests as well (Figure 5-5). Thus, the plant composition of a territory can influence tape distance and hence overall concealment of nests. Territories with an abundance of meadowsweet, rose, and other dense shrubs tended to be more successful because these shrubs obscure the view of the nest better than dogwoods or other more open shrubs such as poison sumac.

Table 5-2. Means (± SE) of tape distance and overhead cover were significantly different between dummy nests that were successful versus depredated. In all cases successful nests were more concealed.

	Dummy Nests				
	Successful	Predated	DF	F-stat	p-value
Tape distance (m)	2.62 ± 0.13	3.64 ± 0.21	82	18.255	< 0.001
Side cover (%)	64.34 ± 2.91	59.55 ± 2.42	36	1.607	0.213
Overhead cover (%)	75.26 ± 3.19	62.16 ± 4.26	36	6.077	0.019

Patterns of vegetation presented in Chapter 3 suggest that first nest attempts were placed at locations within a territory with a greater potential for success. For example, first nest attempts were located in a greater proportion of meadowsweet and rose (Figure 3-8), both of which also show tendencies for greater nest success, especially rose (Figures 3-7, and 3-8). First nest attempts were also surrounded by fewer trees and snags, which, again, were associated with nest predation (Figure 3-12). And while not significant, re-nests were increasingly less concealed than previous attempts (Figure 3-5). These observations lend support to the nest placement hypothesis. However, previous analyses examined changes in variables between individuals and not within individuals. These variations could also be caused by a change in the sample of individuals between nest attempts. For example, the mean increase in number of snags around re-nests could

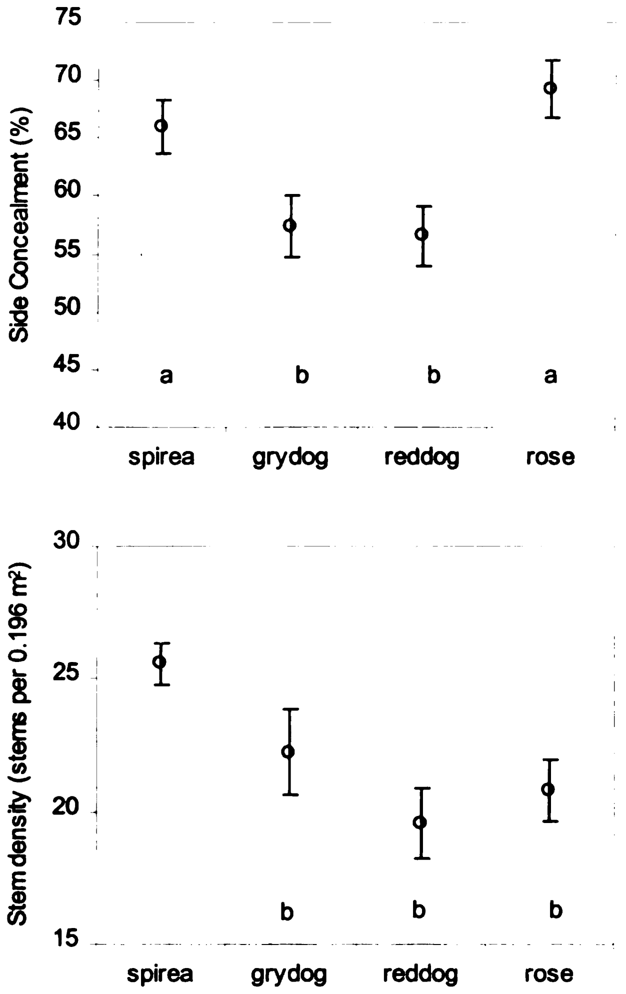

Figure 5-5. YWAR nests in both species of dogwood are significantly less concealed than nests in meadowsweet (spirea) or rose. These nests also have significantly lower stem density surrounding the nest than meadowsweet but not rose. Significance was determined from Fisher's LSD, and is denoted by letters. Error bars are standard error.

be caused by the removal of those successful birds (which do not re-nest) whom had fewer snags surrounding their nests, thus shifting the mean estimate.

If the nest placement hypothesis were valid, we would expect to observe significant changes in nest placement attributes between nest attempts *within* individual birds. Matched pairs Wilcoxon's signed rank tests (non-parametric equivalent to paired t-test) found only the percent coverage of dead plant matter and large trees to be significantly different between first and second nest attempts (Table 5-3). Coverage of dead material diminished as the season progressed, since fresh annual growth tended to replace these areas. The mean difference in number of large trees was small (0.41 trees), which suggests that the significant result for this variable is a product of directional change and not magnitude of change. No other surrounding vegetation classification varied significantly between nest attempts within individuals including the abundance of snags. Moreover, paired t-tests of nest height or stem density around the nest found no significant difference between attempts. These results indicate that within individual nest placement variation does not exist with respect to surrounding vegetation coverage.

Discussion- Results overwhelmingly support the poor parental quality hypothesis. Dummy nests placed in territories of depredated active nests were more likely to become depredated than those on successful territories (Figure 5-2). This pattern suggests that characteristic associated with either the behavior of the parents or the territory they defend increases the risk of nest predation within the territory. The lack of strong relationships between behavioral attributes and nest success (Table 3-10) and the lack of a difference in overall nest predation between dummy and active nests (Figure 5-1),

Table 5-3. Matched pairs Wilcoxon's signed rank tests found that only the coverage of dead plant matter and abundance of large trees significantly changed between first and second nest attempts within individuals. Sample sizes for first, second, and third attempts were n = 158, 76, and 25, respectively.

Vegetation Classification	Attempt 1 vs. Attempt 2		Attempt 2 vs. Attempt 3	
	Wilcoxon Z[a]	p-value	Wilcoxon Z	p-value
Grass/sedge	-0.410	0.681	0.655	0.513
Dogwood/willow	0.827	0.408	0.230	0.818
Meadowsweet	-0.592	0.554	-0.874	0.382
Forb	-1.231	0.218	-0.177	0.860
Rose	1.492	0.136	-0.141	0.888
Other	-0.392	0.695	0.068	0.946
Dead	-2.099	0.036*	-0.277	0.782
Water	-1.734	0.083	1.363	0.173
Snags	0.596	0.551	-0.329	0.742
Small trees	-1.224	0.221	0.844	0.399
Large trees	2.597	0.009**	0.913	0.361

a. Wilcoxon's Z = Sum of signed ranks divided by square root (sum of squared ranks). Positive Z values are increases in coverage or abundance.

suggest that adult behavior is not a proximal factor in nest success. Instead, attributes of occupied territories or nest site selection appear more likely to influence nest success. For example, territories with more snags were more likely to be discovered by cowbirds and nest predators (Figure 3-12). Moreover, territories with more rose overwhelmingly suffered less nest predation (Figures 3-7, 3-8, 3-9). While not significant, territories with less meadowsweet or more dogwood and willow patches had greater nest predation (Figures 3-8, 3-9). With the exception of a small increase in large trees near re-nests, no evidence was found to suggest that changes in nest site selection (Table 5-3), or predator foraging (Figure 5-3) contributed to increased predation for later nests.

Since evidence suggests that avian nest predators are common, it seems plausible that snags and isolated trees serve as perches for potential predators. These avian predators likely include corvids, grackles, and possibly raptors, all of which are much larger than YWAR and locate nests using visual cues. Their greater body size appears to prevent them from finding or getting to nests placed in or near rose. Moreover, nests in dogwood are less concealed than those in rose or meadowsweet (Figure 5-5) making it easier for visually oriented avian predators to locate. Nests on territories with these attributes have a greater probability of becoming discovered by predators. Re-nests by the same individuals have an equally high risk of failure, because they are on the same territory with the same vegetation characteristics.

It remains possible that predatory behavior may contribute to increased predation of re-nests and of dummy nests on territories of failed nests, since some predators may repeatedly return to the territory of a previously discovered nest. However, the existence of other significant relationships that can explain the increased predation of re-nests (see below) and the apparent temporal independence of predation events between dummy and active nest on the same territory appear to refute this.

Age did not appear to influence fecundity directly with respect to egg production or ability to feed young. This is consistent with other YWAR studies (Lozano and Lemon 1999), though not in other species (Saether 1990, Forslund and Part 1995). Alternatively, age of the parents was linked to nest predation (Table 3-7, Figure 3-13). Moreover, while parental behavior at the nest did not differ by age, some habitat attributes were associated with parental age. Specifically, SY adults were more likely to occupy territories with more snags and live trees (Tables 3-8 and 3-9), and less meadowsweet (Figure 3-15). The association of trees and snags to nest predation has already been discussed. Meadowsweet was clearly a preferred nest plant (Table 3-5, Figure 3-10). When I pooled non-use vegetation coverage data for all categories of woody shrubs, I found that ASY females have more shrubs on their territories than SY females (Figure 5-6). Most of these shrubs were preferred nest plants. A greater abundance of preferred nest substrate has been shown to reduce the risk of nest predation, by increasing the predator's search area (Martin 1993b).

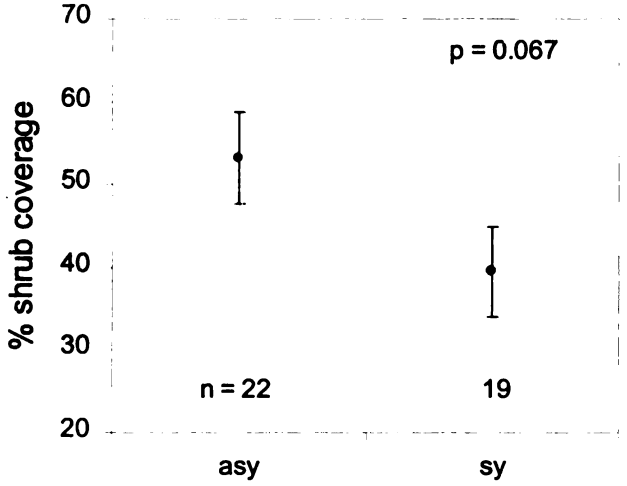

Figure 5-6. Shown here is the total percent cover of all woody shrub vegetation for non-use samples compared with age of female YWAR. ASY females had marginally significantly more shrubs on their territories than SY females.

These results suggest that older adults did better than younger adults because they were able to obtain and defend the best territories within a habitat. Consequently, SY adults suffered greater nest predation because they occupied lower quality habitat. These birds represented a greater proportion of re-nests (Figure 3-14) and their re-nests inherently had a high risk of predation (Figure 3-3) due to their association with lower quality habitat.

This pattern is consistent with the constraint hypothesis for explaining age-specific variation in reproductive success. This hypothesis states that age-specific difference in reproductive success exists because younger individuals are unable to reproduce as well as older ones because they are less capable of competing for the best breeding territories (Curio 1983, Forslund and Part 1995). Evidence to support this hypothesis have been documented in the Great Tit (Harvey et al 1979), Black-headed Grosbeak (Hill 1988), American Redstart (Lemon et al. 1996) and even other populations of Yellow Warbler (Lozano and Lemon 1999). Younger birds, due to their inexperience, unfamiliarity with the habitat, and/or inability to arrive as soon as older adults are left with the lower quality sites within the habitat.

Improvements and future research- Several suggestions can be made to improve future studies attempting to identify the array of factors influencing seasonal fecundity. Complete vegetation assessment of dummy nests was not performed in this study. To do so would have permitted more detailed comparisons of vegetation characteristics that influence nest success. In general, field studies should not ignore detailed vegetation assessment. In addition to measurements made in this study I suggest including more non-use sampling (especially within territories), measurements of vegetation stratification, and measuring territory size as an alternative index to territory quality. Additional measurements should include more detailed behavioral assessment, including longer observation periods and other behaviors such as vocalization. Arrival dates of individuals should be documented when possible. This would help determine if those that arrived first selected the best territories.

Additional questions, which were derived from this study, should also be explored in the future. For example, in 1999, there was a period during early June when no re-nesting occurred following failure, an event not observed in any other year. Apparently, high ambient temperatures during this time period contributed to this since only those nests that failed then did not re-nest. Those that failed the following week in cooler weather did re-nest. Given the important role re-nesting has on fecundity, will global climate change have a dramatic impact on some songbird populations? It was also discovered that nest abandonment does not necessarily improve fecundity, and nests that were abandoned varied in concealment relative to nest that were not. The decision to abandon or not may depend on the parents assessment of the potential for success of the current nest attempt versus future nest attempts. Answering such questions will improve our understanding of how nest predation and brood parasitism interact to influence fecundity, and thus improve our ability to preserve and protect bird populations.

CONCLUSIONS AND RECOMMENDATIONS

Nest predation and brood parasitism clearly do not interact in such a way as to compound their effect on seasonal fecundity. Moreover, the combined effect of the two is less than the sum of the effects of each of the parts. For example, a population exposed to a moderate to high parasitism rate may perform equally well reproductively at either 20% or 50% nest predation frequency, while a population not exposed to parasitism may show a decline in fecundity between the same two nest predation frequencies. Likewise, a population exposed to moderate to high nest predation will be less affected by a 50% parasitism rate than a population exposed to a low predation rate. These two phenomena interact antagonistically to reduce the effect of the other on seasonal fecundity.

This antagonistic interaction results from the fundamental difference in a host bird's response to each phenomenon, namely the re-nest response. Single-brooding songbirds are able to recover much of the loss in fecundity from nest predation through re-nesting, but cannot recover losses from parasitism unless the parasitized nest is depredated or otherwise abandoned. For those species that do not frequently abandon parasitized nests, nest predation is the most common means of escaping parasitism. Thus nest predation can recover some of the potential loss due to parasitism.

Moreover, under specific conditions, increasing nest predation may actually lead to slight increases in seasonal fecundity in a population. This special case can exist when brood parasitism frequency is high, generally greater than 70%, and costly, generally greater than 80% reduction in brood size. This effect of nest predation is most likely to occur in populations that have greater nest predation on parasitized nests and have greater nest survival for re-nests. In theory, it is possible for all these conditions to occur simultaneously in a single population but is likely uncommon. While not observed in this study population, locally high parasitism rates of Yellow Warbler and other small migrant songbirds are common, and many of these species frequently exhibit severe reductions in brood size when parasitized. In addition, nest predation can be higher for parasitized nests, as was the case in this study. However, greater nest success for re-nests does not appear to exist, and in fact was observed to be just the opposite. Lower nest success for re-nests can by itself preclude nest predation from increasing fecundity in any parameter space.

The lack of studies that clearly differentiate re-nests from initial attempts prevents an assessment of how frequent this pattern exists in other natural populations, but greater predation on later nests has been documented in other species (Beaver 1975). Field observations and experimentation with the Yellow Warbler seem to suggest that greater nest predation on re-nests resulted from a shift in composition of breeding adults. Only those birds that failed in their first nest attempt would re-nest. This changed the proportion of individuals in re-nests. Characteristics of these individuals, namely age, and quality of the territories they occupy, led to a greater risk of nest failure. Thus re-nests did not necessarily suffer an increased predation rate relative to first nest attempts, but instead suffered greater predation because there were composed of a greater proportion of parents that were inherently inferior.

The relationship of habitat quality with nest success and the association of parental age with territory quality are well documented in birds (Hinde 1956, Brown 1969, Curio 1983). Therefore it would appear reasonable to expect increased predation on re-nests to be frequent in single-brooding songbirds. Greater nest predation on re-nests can prevent the manifestation of a population wide increase in fecundity at intermediate nest predation. Thus no level of nest predation is likely to increase seasonal fecundity in populations. If this effect does occur, it is likely rare and inconsequential to most bird populations, especially those with a large proportion of young adults that would lead to greater re-nest predation.

Regardless, while nest predation may not increase seasonal fecundity when re-nests have lower success, nest predation still does not greatly reduce seasonal fecundity when parasitism is frequent. Thus the interaction of these two phenomena can still have important consequences to a population. Those populations experiencing moderate to high parasitism will not be affected by an increase in nest predation through a range below 60%. Moreover, the benefit of nest predation can still exist at the individual level. For example, in at least three cases yellow warblers fledged three young following predation of their parasitized nest. This was greater than the average brood size of successful parasitized nests, suggesting these birds gained from nest predation. However, the vast majority of parasitized nests that were depredated never successfully fledged young because their re-nests were repeatedly depredated.

The consequences of nest predation and brood parasitism on nesting success in birds have been a significant focus of theory (Pease and Grzybowski 1995, Schmidt and Whalen 1999). However, the interaction of nest predation and brood parasitism is largely unexplored in field studies. The main reason for this appears to be the lack of focus in nest success studies on differentiating nest attempts. This appears to be due to the great effort involved in doing so. In concurrence with other authors working on this problem (Pease and Grzybowski, in press), I recommend that more emphasis be placed on assessing the impact of nest predation and brood parasitism on seasonal fecundity instead of on individual nest success. This will require careful nest searching and monitoring to properly identify each nest attempt made by individual birds. Tracking each nest attempt is easier in populations that exhibit strong territoriality, remain on the same territory during all breeding activity, and in habitats where territory boundaries are clearly identifiable. Extensive color banding efforts also help to identify and track individuals and their nest attempts. While challenging this is not impossible and can be done with limited resources as demonstrated in this study. By utilizing voluntary labor, this research was done with an annual budget under $1,000 and with three or fewer volunteers each year.

As demonstrated here, a myriad of secondary factors influence how nest predation and brood parasitism interact. Variations in these conditions clearly exist both spatially and temporally. Management practice would benefit from a better understanding of the interaction of nest predation and brood parasitism as well has an understanding of temporal changes in nest success and the factors involved. Clearly, as others have stated, the best management practice is to preserve large areas of high quality habitat, since this greatly reduces the risk to both nest predation and parasitism simultaneously. However, this option is rarely available and is costly. Therefore more hands-on management practices are often used, at least for short-term recovery while habitat is restored. For example, cowbird removal has been used to improve reproductive success in some songbirds (Robinson et al. 1993). However, the results of this management practice have been mixed. While cowbird removal has helped the Kirtland's Warbler (Walkinshaw 1983) it had no affect on the Hooded Warbler despite sharply reducing parasitism events

(Stutchbury 1997). The decision to manage cowbird abundance as a means of improving nesting success must depend on other factors in the target population, especially nest predation. Other factors to consider include age structure, and habitat quality, as well as life history traits such as the frequency of re-nesting, and whether they double-brood.

Because of the complexity of the interactions involved, simulation modeling will be an increasingly powerful tool for managers. Simulation models that allow for easy manipulation of parameters, such as in FLEDGE, will help identify those parameters that will result in the greatest change in seasonal fecundity. In this way, managers can focus on specific aspects of the target population and more efficiently use available resources. In general, managers will have to take into account the fact that nest predation and brood parasitism reduce the effect of the other. As one factor is diminished the effect of the other is likely to increase. In addition, general management practices will likely benefit from focusing on improving habitat quality. This may initially cost more but will have long-term positive results and savings, since more quality habitat, even locally, will likely improve reproductive success, and will require minimal hands-on management to maintain.

APPENDIX

Table A-1. Each column in the body of this table includes the parasitism frequency values used for plotting graphical input of a declining brood parasitism probability. Frequencies down a column change by the same given percent.

	Initial Percent Parasitism				Percent
Day	20%	40%	60%	80%	of decline
0	0.200	0.400	0.600	0.800	--
10	0.200	0.400	0.600	0.800	0%
20	0.184	0.368	0.552	0.736	8%
30	0.160	0.320	0.480	0.640	20%
40	0.130	0.260	0.390	0.520	35%
50	0.080	0.160	0.240	0.320	60%
60	0.030	0.060	0.090	0.120	85%
70	0.00	0.00	0.00	0.00	100%
80	0.00	0.00	0.00	0.00	100%
90	0.00	0.00	0.00	0.00	100%

Table A-2. Each column in the body of this table includes frequency values used to plot a decreasing nest predation function for four initial predation levels. Frequencies down a column change by the same given percent.

	Initial Percent Predation				Percent
Day	10%	30%	50%	70%	of decline
0	0.100	0.300	0.500	0.700	-
10	0.100	0.300	0.500	0.700	0%
20	0.095	0.285	0.475	0.665	5%
30	0.085	0.255	0.425	0.595	15%
40	0.066	0.198	0.330	0.462	33%
50	0.055	0.165	0.275	0.385	45%
60	0.050	0.150	0.250	0.350	50%
70	0.050	0.150	0.250	0.350	50%
80	0.050	0.150	0.250	0.350	50%
90	0.050	0.150	0.250	0.350	50%
100	0.050	0.150	0.250	0.350	50%

Table A-3. Each column in the body of this table includes the values used to plot the re-nest frequency function, r(t), used in simulations of altering the probability of re-nesting.

Day	Initial Re-nest frequency				Percent of decline
	30%	50%	70%	100%	
0	0.30	0.50	0.70	1.0	-
10	0.30	0.50	0.70	1.0	0%
20	0.30	0.50	0.70	1.0	0%
30	0.30	0.50	0.70	1.0	0%
40	0.30	0.50	0.70	1.0	0%
50	0.24	0.40	0.56	0.80	20%
60	0.0	0.0	0.0	0.0	100%
70	0.0	0.0	0.0	0.0	100%
80	0.0	0.0	0.0	0.0	100%
90	0.0	0.0	0.0	0.0	100%
100	0.0	0.0	0.0	0.0	100%

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