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Breeding biology of birds in a Western riparian forest: From demography to behavior

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BREEDING BIOLOGY OF BIRDS IN A WESTERN RIPARIAN FOREST – FROM DEMOGRAPHY TO BEHAVIOR

By

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B.A. Prescott College, USA 1992

Presented in partial fulfillment of the requirements for the degree of Doctorate of Philosophy

The University of Montana

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Breeding Biology of Birds in a Western Riparian Forest – from Demography to Behavior.

Director: Thomas E. Martin TEM

Nest predation and brood parasitism are the two primary processes influencing the reproductive success of birds. I studied these processes in the Bitterroot Valley of Western Montana. With a large crew of field assistants, I conducted point-count surveys at 206 locations, monitored the success of 3079 nests of 78 species, and banded 596 Yellow Warblers and American Redstarts from 1995 through 1999 in deciduous forest habitats surrounded by landscapes ranging from heavily fragmented by agriculture to completely surrounded by forest. In addition, I conducted experiments to determine the effect of parasitism on incubation rhythms of Yellow Warblers.

Predation rates were higher in forested landscapes than in fragmented landscapes dominated by agriculture, likely reflecting the importance of forest predators in these landscapes. The strongest predictor of brood parasitism by Brown-headed Cowbirds (*Molothrus ater*) was the abundance of human development (farms and houses). The combined effects of predation and parasitism resulted in low nesting productivity in both forested and agricultural landscapes for heavily parasitized species, while the species not affected by cowbird parasitism had greater nesting productivity in fragmented agricultural landscapes.

The distance to agricultural areas was the strongest predictor of cowbird occurrence and relative abundance across out study location. In addition, cowbirds were almost never encountered within steep-sided canyons. Outside of canyons, host density and vegetation type influenced cowbird abundance, with more cowbirds in deciduous riparian areas and areas of higher host density. The number of female cowbirds detected on point counts provided the best fit with parasitism frequency, suggesting that sex determination during cowbird surveys will improve predictions of parasitism rates. Parasitism frequency was best predicted at a 1 km radius landscape scale.

My experiments demonstrated that egg-removal causes fitness costs for yellow warblers, and Yellow Warblers respond to the threat of egg-removal by increasing attentiveness on the nest. Increased attentiveness reduces risk of egg removal, but requires males to feed females more often. This increased visitation rate of the male increases nest predation. Thus birds are caught between the cost of egg-removal by brood parasites and the cost of increased nest predation when they attempt to reduce egg-removal.

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Chapter 1

Habitat Fragmentation in a Western Landscape: Breeding Productivity does not Decline with Increasing Fragmentation

Abstract

Fragmentation of breeding habitat may cause declines in many bird populations. Our perception of the demographic effects of habitat fragmentation comes primarily from studies in the Midwestern and eastern United States and Scandinavia. We know very little about the demographic effects of anthropogenically caused habitat fragmentation in habitats prone to natural disturbance, as is typical of most forest types in the western United States. We located and monitored 1916 nests on eight sites located in mostly forested landscapes, and eight sites located in primarily agricultural landscapes to study the effects of landscape level fragmentation on nest predation and brood parasitism in riparian areas in western Montana.

Patterns of nest predation were opposite those documented from more eastern locales; predation rates were higher in forested landscapes than in fragmented landscapes dominated by agriculture. This pattern probably reflects the importance of forest predators in these landscapes: red squirrels (*Tamiasciurus hudsonicus*) were much more abundant in forested landscapes and declined quickly with decreasing forest cover, whereas predators that typically increase in fragmented landscapes in the Midwest (such as corvids) increased only at very high levels of fragmentation. Patch size and distance to habitat edge did not influence predation rates. Brood parasitism by Brown-headed Cowbirds (*Molothrus ater*) decreased with increasing forest cover, but the strongest predictor of parasitism was the abundance of human development (farms and houses) on the landscape and the density of cowbird host species, not forest cover. The combined effects of predation and parasitism resulted in low nesting productivity in both forested and agricultural landscapes for heavily parasitized species, while the species not affected by cowbird parasitism had greater nesting productivity in fragmented agricultural landscapes. Our results suggest that the effects of fragmentation are dependent on the habitat structure, the landscape context, the predator community, and the impact of parasitism. All of these factors may differ substantially in western ecosystems when compared to previously studied forests, making generalizations about the effect of fragmentation difficult.

Key words: landscape fragmentation, nest predation, brood parasitism, riparian birds, Yellow Warbler, Warbling Vireo, American Robin, Cedar Waxwing.

Key Phrases: forest fragmentation in the west: affects on birds; nest predation vs. landscape change; brood parasitism vs. human habitation and host density.

Introduction

Much of our understanding of the demographic effects of fragmentation comes from studies of bird populations (Ambuel and Temple 1983, Brittingham and Temple 1983, Howe 1984, Wilcove 1985, Temple 1986, Askins et al. 1990, Freemark and Collins 1992, Robinson 1992, Villard et al. 1992, Faaborg et al. 1995, Robinson et al. 1995, Brawn and Robinson 1996). Most of these studies focus on edge and patch size effects, but the composition of landscapes surrounding remaining fragments also can be important; studies in midwestern North America have shown that lower forest cover on the landscape is correlated with both higher nest predation and higher brood parasitism (Donovan et al. 1995, Robinson et al. 1995).

Landscapes in the eastern half of the United States historically were blanketed by contiguous hardwood forest, but many of these landscapes are now highly fragmented and remaining forest patches are often surrounded by agriculture (Donovan et al. 1995,1997, Robinson et al. 1995). In contrast, forest habitats in the western United States are often naturally patchy from extensive topographic variation and periodic disturbance from fire and flooding (Hejl 1992, 1994, Attiwill 1994, Ohmart 1994). Riparian habitats typify the patchy character of many western habitats and, in fact, tend to be patchy throughout the world. The demographic effects of human induced fragmentation in these naturally fragmented habitats may differ substantially from the effects seen in midwestern and eastern North America.

Increases in both nest predation and brood parasitism have been repeatedly correlated with habitat fragmentation (Gates and Gysel 1978, Wilcove 1985, Gates and Griffen 1991, Brittingham and Temple 1983, Paton 1994, Robinson et al. 1995, Donovan et al.1997). However, many studies have relied on indirect data such as artificial nests

(Wilcove 1985, Ratti and Reese 1988, Donovan et al. 1997; see Paton 1994 and Andrén 1995 for reviews of results from artificial nest studies), which may not reflect actual predation rates (Martin 1987, Willebrand and Marcström 1988, Roper 1992, Haskell 1995). Additionally, most studies have considered only local habitat characteristics, such as nest concealment, edge effects and patch size effects, without considering landscape context (Andrén 1995). The abundance of predators and cowbirds in an area may depend more on characteristics of the surrounding landscape than on patch-specific habitat features, and thus the composition of larger landscapes may be critical in shaping predation and parasitism patterns at local scales (Andrén 1995, Donovan et al. 1997).

We explored patch size, edge, and landscape effects on nest predation and brood parasitism in deciduous riparian systems in western Montana and examined the demographic consequences for bird populations. Deciduous riparian habitats make up less than 1% of the western United States (Szaro 1980), yet they are the primary breeding grounds of more than 60 percent of the passerine bird species in the western United States (Johnson et al. 1977, Knopf 1985, Knopf et al. 1988, Dobkin and Wilcox 1986, Saab and Groves 1992, Bock et al. 1993, Ohmart 1994). Here we provide the first study to examine the demographic consequences of landscape fragmentation around these critical western riparian habitats. We provide an important test of the generality of eastern fragmentation models by examining fragmentation effects in riparian habitats in the western United States where both historical and current landscape patterns differ substantially from the Midwest and East.

Methods

Study area and study sites

Study sites were located in the southern Bitterroot Valley, 70 kilometers south of Missoula, Montana. Ranches, agricultural fields and small towns dominate the valley. Forest cover increases west of the Bitterroot Valley in the foothills of the Bitterroot Mountains. This area is mostly Bitterroot National Forest land, managed for multiple use, timber production and Wilderness. Where National Forest land meets private land, a rough forest - farmland interface is formed (Fig. 1A).

Sixteen study sites were established, eight in highly fragmented, agricultural landscapes along the Bitterroot River, and eight in largely unfragmented forested landscapes along smaller streams in the foothills of the Bitterroot Mountains. (Fig. 1). These two landscape types (forested and agricultural) will be considered landscape treatments for examination of nest predation. Forest fragmentation does not occur randomly and any large-scale examination of the effects of fragmentation must use existing landscape patterns. While no study has completely controlled for local differences between study locations unrelated to landscape features, we selected study sites to minimize differences on sites while still encompassing the full range of variation in landscapes surrounding sites. Though vegetation differences among sites were unavoidable, these differences were not strongly correlated with landscapes features and did not explain differences in predation and parasitism among sites.

Sites averaged 12 ha in size and ranged in elevation from 1050 to 1350 m. All sites were dominated by deciduous trees and shrubs typical of either the black cottonwood (*Populus trichocarpa*) / red - osier dogwood (*Cornus stolonifera*) community type (Hansen et al. 1995), the quaking aspen (*Populus tremuloides*) / red - osier dogwood

(*Cornus stolonifera*) habitat type, or the mountain alder (*Alnus incana*) community type (Hansen et al. 1995). All study sites were located in the same broad valley (Fig. 1A), thus differences in predator and cowbird densities among sites reflect functional and numeric responses to local landscape and habitat differences, rather than differences in the regional abundance of predators and cowbirds caused by landscape variation at larger scales. However, our study sites are far enough apart to insure general independence of major predators and cowbirds among sites. Elsewhere, cowbirds have been shown to move large distances between feeding and breeding areas (Thompson 1994). However, where cowbirds have feeding and laying resources in close proximity, as we find in the Bitterroot Valley, they often move much smaller distances between feeding and laying areas (Thompson et al. 1994). We used radio-telemetry to track nine female cowbirds laying on our study sites and found that no cowbirds used more than one area for breeding, and breeding ranges were less than 500m long (Tewksbury unpublished data). Additionally, cowbird movements between breeding and feeding areas were generally less than 1 km as found elsewhere (Thompson et al. 1994), suggesting that cowbird numbers and parasitism on sites was a function of local landscape character, and sites were generally independent. To maximize our ability to detect landscape effects on predation and parasitism, we focused our analysis on species found in both fragmented, agricultural landscapes and unfragmented forested landscapes.

Landscape metrics

Habitat type and land-use coverages were developed for the study area and entered into a Geographic Information System using PC ARC/INFO (ESRI 1989). We obtained habitat and land use data by examining 1:15840 aerial photographs and delineating habitat polygons on orthophotographs. To verify habitat and land use types, we field-checked all mapped polygons during the study. A total of 31 different habitat types were described (Appendix A). The local landscapes around each of the 16 study sites were defined at two spatial extents: all land within 1 km from the perimeter of the site (1 km extent - Fig. 1), and all land within 2 km from the perimeter (2 km extent). Larger landscapes were not considered because the observed variation in predation and parasitism rates could not be accounted for by using larger landscape scales as the proximity of study sites created overlap in landscape area and homogenized, rather than differentiated landscapes. FRAGSTATS spatial analysis software (McGarigal and Marks 1995) was used to compute landscape metrics around each site at both landscape extents. Percent cover of the major habitat types consistently portrayed the overall character of the landscape regardless of changes in landscape extent, while other metrics generated by FRAGSTATS, such as habitat patch size and habitat patch density, were difficult to interpret and dependant on the landscape extent. Therefore, all landscape metrics analyzed are the percent of the local landscapes covered by the habitat or land use type of interest.

Patch size and edge effects

The deciduous riparian habitats of our study are naturally fragmented by river channels and other vegetation types, and thus fifty five percent of all nests monitored were within 100m of some edge type, and very few nests were further than 200m from some edge. To examine patch size and edge effects, we defined the patch size of our study sites as the area of deciduous vegetation bounded on all sides by any other habitat type (agriculture, coniferous forest) or a river channel greater than 25 m wide. We measured the distance to the two closest edges within 100m of each nest, and did not consider adjacent habitat further than 100m from the nest. Edge types considered here include deciduous riparian habitat abutting agricultural fields, water, coniferous forest, and meadows.

Variables influencing predation and parasitism

The percentage of local landscapes covered by forest has been used most often to quantify habitat fragmentation in relation to nesting success and brood parasitism (Andrén 1992, Robinson et al. 1995, Donovan et al. 1995). We therefore examined the relationship between percent forest cover and both nest predation and brood parasitism. However, we found cowbirds most often feeding in areas associated with human habitations, such as farms and houses, not simply landscapes with low forest cover. The Bitterroot Valley is predominantly rural, and most houses have either a small corral, or an area where chicken or wild bird food is abundant. Cowbirds use all these resources for feeding. Consequently, we designated human habitation as all development, including farm buildings, corrals, livestock holding areas, and residential development, and included this metric in our analysis of brood parasitism. We analyzed percent cover of human habitation rather than actual density to be consistent with other landscape metrics. Thus the importance of an individual farm is a function of its size, and a landscape with larger farms has more human habitation than a landscape with an equal number of smaller farms (Fig. 1B and 1C).

Assessing predation rates, parasitism rates, and relative abundance

During the 1995 and 1996 breeding seasons, a total of 1916 nests of 74 species were found and monitored to determine fledging success and parasitism using methods described in Martin and Geupel (1993).

Nest fate was determined by checking nest status every two to four days. Most nests were approached at least once to determine clutch size. We used mirror poles and ladders to access high nests. We modified fate protocols established by Martin et. al. (1996), to account for cowbird parasitism and provide a standardized decision tree for nest fate determination that minimized bias. Predation was assumed when the nest was torn apart, destroyed or found empty with no sign of inclement weather, after the first egg was laid and before the expected fledge date. Predation rates were estimated using the Mayfield Method (Mayfield 1961, 1975) as modified by Hensler and Nichols (1981). This method determines the nests lost per day of nest exposure to correct for potential biases associated with finding some nests later in the nesting cycle (any day after the first egg is laid). Predation was determined on a treatment level (8 sites embedded in forested landscapes vs. 8 sites in agriculturally dominated landscapes - Fig. 1) for the American Robin (*Turdus migratorius*), Cedar Waxwing (*Bombycilla cedrorum*), Warbling Vireo (*Vireo gilvus*), Yellow Warbler (*Dendroica petechia*), and Back-headed Grosbeak (*Pheucticus ludovicianus*), the only five open-cup nesting species that were sufficiently abundant in both treatments. Cavity-nesting species are not considered in this paper.

Brood parasitism by the Brown-headed Cowbird was determined for 550 nests. The percentage of nests parasitized was measured on a site by site basis both by pooling nests across all prime host species (Table 1) and by examining parasitism rates on Yellow Warblers and Warbling Vireos separately. These species were the only two sufficiently abundant to allow us to estimate parasitism rates across individual sites. Parasitism rates reported are the percentage of nests parasitized, rather than a daily parasitism rate (Woodworth *In press a*). Though daily parasitism rates may correct for potential bias associated with differing periods of susceptibility to brood parasitism (Pease and Gryzbowski 1995), the percentage of nests parasitized on our sites was highly correlated with daily parasitism (Pearson's correlation; $n = 16$, $r = 0.95$ $P < 0.0005$ for all hosts, $n = 9$, $r = 0.90$, $P = 0.001$ for Yellow Warblers, and $n = 8$, $r = 0.87$, $P = 0.005$ for Warbling Vireos). Thus the use of daily parasitism would not improve our analysis or change our results, and interpretation would be more difficult. Neither the percentage of nests parasitized nor daily parasitism accounts for the potential bias that may result when nests are found after clutch initiation and many nests are abandoned early in the nesting cycle due to parasitism. When this occurs, reported rates of parasitism may be less than actual parasitism, as nests found later in the nesting cycle are more often unparasitized. To examine this possibility, we compared parasitism rates for all nests monitored with parasitism rates calculated using only nests found before clutch initiation.

We conducted point count surveys of all birds on all sites over the two seasons. Following methods outlined in Hutto et al. (1986), each point count location was censused three times per season, each count was 10 minutes long, and all birds seen or heard in a 50 m radius from the point were recorded. Relative abundance was determined from a total of 450 counts censused on 82 point locations between dawn and 11:00 A.M.. Point locations were systematically distributed on sites such that each point was greater than 200 m from all other points. The number of points per site varied from 2 to 8 as a function of site size. We examine the relationship between the relative abundance of the two most common predators on our sites, Red Squirrels (*Tamiasciurus hudsonicus*) and

Black-billed Magpies (*Pica pica*), and landscape features. Though other predators were also present in lesser numbers, these two species made up over 90% of all predator detections. We also present relative abundance of cowbirds and cowbird hosts. We considered all species in which greater than 15% of nests were parasitized in this analysis (Table 1, prime hosts). In our analysis of the effect of host density on brood parasitism rates, we calculated the estimated marginal mean of host density on each site (total host detections per point location divided by the number of points) from an ANOVA with year and site included as main effects.

We tested for between year variation in cowbird abundance, predation rates, and parasitism rates, as an interaction between annual variation and study site or landscape treatment could confound our results if years are pooled. If no interaction is observed, annual variation in these metrics makes detection of biological differences more difficult, but will not confound results.

Nesting productivity

Nest predation and brood parasitism accounted for greater than 90% of nest losses. As these processes may interact to reduce annual fecundity, we examined the joint impact of these processes on four species common to both landscape types; two that are rarely parasitized and reject cowbird eggs (American Robin and Cedar Waxwing), and two that are heavily impacted by brood parasitism (Warbling Vireo and Yellow Warbler). We did not include Black-headed Grosbeak in this analysis as our information on parasitism rates for this species is not complete. We constructed a simple model incorporating our data on predation pressure and parasitism rates in the two landscape treatments with the effect of parasitism on the number of young fledged from successful nests. By combining these data, we estimated the mean number of young fledged per nesting attempt in both forested landscapes (F_F), and agricultural landscapes

$$F_F=(NS_F*SP_F*F_{wp})+(NS_F*(1-SP_F)*F_{np})$$

$$F_A=(NS_A*SP_A*F_{wp})+(NS_A*(1-SP_A)*F_{np})$$

Where *NS* is Mayfield adjusted nesting success in each landscape treatment, *SP* is the proportion of successful nests parasitized in each landscape treatment, F_{wp} is the average number fledged for parasitized nests and F_{np} is the average number fledged for unparasitized nests. This approach incorporates Mayfield adjusted nesting success and partitions the effects of parasitism and predation, thus it is less biased and more flexible than the standard approach of simply dividing the total number of young fledged for a species by the number of nests monitored. However, nesting productivity should not be confused with seasonal reproductive success, which must account for re-nesting effort. We do not address seasonal reproductive success here.

Data Analysis

Our examination of predation included one paired t-test of landscape treatment, four ANOVA tests of edge type and one regression of predation rate vs. patch size. To correct for inflation of significance due to multiple testing, we use sequential Bonferroni adjustment of significance (Rice 1989) for the 6 tests. To examine parasitism, we tested forest cover, host density and the extent of human habitation. Prior to analysis, percentile metrics were arcsine square root transformed where necessary (Zar 1984). All three of these tests were conducted with all primary host species pooled and for two individual species for which we had sufficient sample size (9 tests). We also examined the independent effects of forest cover and human habitation on parasitism rates on all primary hosts pooled. Correction for multiple tests is thus based on 11 tests.

To determine the landscape size which best predicted predator and parasite densities on our sites, we used the GLM procedure in SPSS version 7 (SPSS inc. 1996) and the percent cover of habitat types at both the 1 and 2 km landscape extents. Using type I sums of squares, we forced a landscape variable at the 1 km extent first and then added the same variable at the 2 km extent. We then reversed the procedure, first forcing the variable at the 2 km extent and adding the 1 km extent second (Table 2). Landscape features were highly correlated between spatial extents (Pearson's correlation coefficient > 0.75 in all cases), primarily because the larger landscape extent includes the smaller landscape. Therefore, the extent entered first always explained the vast majority of variation in predator and parasite numbers (Table 2). However, variation in Brown-headed Cowbird and Red Squirrel densities on our sites were slightly better explained by forcing the 1 km landscape extent first, while magpie detections were slightly better explained by forcing the 2 km extent first (Table 2). Because 1 km extents provided a better fit for the most abundant predator censused and for cowbirds, we use 1 km landscapes for all following analyses. However, our results do not change when the 2 km extent is used.

Differences in predation rates between years and between species and landscape types were examined using program CONTRAST (Hines and Sauer 1989), which uses a Chi-square statistic to test for homogeneity of survival rates by creating a linear contrast of the rate estimates (Sauer and Williams 1989). Differences in predation rates between forested landscapes and fragmented agricultural landscapes were examined using a paired t-test on mean daily predation rates blocking by species and testing for a landscape affect. The five most abundant species were included in this analysis.

For analysis of the effects of edge on predation rates, we calculated exposure days as the number of days the nest was active from first egg laid until the date of predation or success. We restricted our analysis to nests found on or before the third day of incubation that had either failed due to predation or were successful. As these data were normally distributed, edge distance was used as a covariate in an ANCOVA design in which site and species were included as main effects to control for differences between landscapes and species. The hypothesis that smaller patches would have higher predation rates was examined using linear regression for the five most common species combined, as well as for American Robins separately, as they were the only species with sufficient nest numbers to be compared across plots.

Forest cover and agricultural land were strongly related (Pearson's Correlation n = 16, r = -0.826, $P < 0.0005$). These two variables essentially index the same landscape variation, and so only forest cover is tested, to allow comparisons with previous studies. We used partial regression analysis to examine the independent relationships between parasitism and forest cover, patch area, and human habitation; testing each while controlling for the effects of the other two variables. Thus the partial F statistic and associated partial R^2 for each landscape variable measure the additional explanatory contribution of that variable after the effects of the other variables have been accounted for. We used the same technique to separate cumulative host density and human habitation to examine their independent effects on parasitism rates.

Results

Annual Variation

Nest predation did not differ between years for any of the individual species or for all species combined (χ^2 $P > 0.15$ in all cases). Brood parasitism also did not differ between years for either of the two species analyzed separately or for all prime hosts combined (χ^2 $P > 0.2$ in all cases). We therefore pooled data from both years. Neither predator (Red Squirrel or Black-billed Magpie) showed significant variation between years (Mann-Whitney U: Red Squirrel $P = 0.41$, Black-billed Magpie $P = 0.15$). Cowbird abundance was higher in 1996 (ANOVA $F = 10.6$, $df = 1{,}35$; $P = 0.003$), but no interaction was found between year and site ($F = 0.568$, $df = 14{,}55$; $P = 0.878$). Cumulative host density was also higher in 1996 (ANOVA $F = 6.13$ $df = 1{,}20$; $P = 0.022$) but we found no interaction between year and site ($df = 14{,}54$, $F = 1.291$, $P = 0.24$). Therefore site differences were independent of yearly variation in both cases, and years were pooled.

Predation

Nest predation was higher in forested, less fragmented landscapes than in agricultural landscapes ($t = 6.3$, $P = 0.003$, Fig. 2). Every open-cup nesting species with sufficient sample size (>=30 nests) showed the same trend. Predation rates may vary for a number of reasons, but predator densities may explain much of the variance in our system. Red Squirrel density was much higher in forested landscapes ($r^2 = 0.53$, $P = 0.001$ - Fig. 3A), while magpies were only found on sites with extremely low forest cover (Fig. 3B). However, the overall relative abundance of red squirrels was 10 times greater than magpies, and squirrels outnumbered magpies on all but two sites (paired t-test t = 3.98, df 15, $P = 0.001$).

Predation rates were not affected by the distance from any habitat edge types tested (Table 3). Patch size also showed no relationship with predation pressure either on American Robins ($r^2 = 0.06$, $df = 12$, $P = 0.4$) or all five species combined ($r^2 = 0.11$, $df = 13$, $P = 0.254$).

Parasitism

Brown-headed Cowbirds regularly parasitized 16 primary host species on our sites (Table 1). Parasitism rates did not change substantially for any species when the analysis was restricted to nests found before clutch initiation (Table 1, Pearson's χ^2, all P's > 0.2), and so all further analyses are conducted on the larger sample of all nests.

Parasitism decreased with higher forest cover when all prime host species were considered together (Fig. 4A). However, though the same trend is apparent for individual species, the relationship was not significant after correction for multiple tests (Fig. 4B - 4C). Forest cover and human habitation were positively correlated, and when we included forest cover, patch size, and human habitation in a partial regression analysis, human habitation was the only landscape variable explaining variation in parasitism rates among sites (Table 4). We therefore used human habitation instead of forest cover in all further analyses of parasitism.

When we combined all host species and examined parasitism pressure in relation to both human habitation and cumulative host density both independent relationships were highly significant (Fig. 5A and 5B). When we considered species individually, both relationships remained highly significant (Fig. 5C through 5F) and the predictive strength of both relationships generally increased (Fig. 5C, 5D, and 5F).

Nesting productivity

Nesting success of Cedar Waxwings in agricultural areas was almost twice as high as in forested landscapes, where less than 25% of nests were successful (Table 5). Similarly, American Robin nesting success was higher in fragmented landscapes dominated by agriculture. As a result, the number of young fledged per nesting attempt was less in forested landscapes for both these species (Fig. 6). Neither of these species were affected by brood parasitism, and thus this difference was due almost entirely to higher nest predation in forested landscapes (Fig. 2). In contrast, Yellow Warblers and Warbling Vireos are both heavily parasitized and showed equally low nesting productivity in both landscapes (Fig. 6). However, the causes of low productivity were different in these two landscapes. In fragmented landscapes, nest predation on Yellow Warblers and Warbling Vireos was lower than in forested landscapes, as seen with the non-parasitized species, but nest loss due to parasitism was much higher. We considered two ways in which parasitism decreases nesting productivity: nest failure due to abandonment or death of all natal young, and reduction in the number of young fledged from successful nests due to cowbird egg ejection and competition with cowbird nestlings. Both of these factors decreased nesting productivity further in fragmented landscapes (Table 5) where cowbirds are more abundant. Increased parasitism in fragmented landscapes may also reduce re-nesting potential, as birds that only fledge cowbirds are constrained by fledgling care, just as birds raising natal fledglings, and thus may not re-nest. This impact is not considered in the current paper.

Discussion

Predation

Studies from the midwestern United States suggest that predation rates increase rapidly with decreasing forest cover and increasing agriculture on the landscape (Andrén 1992, Donovan et al. 1995, Robinson et al. 1995). We found the opposite. For the five most common species present across both landscapes, nest predation was greater in predominantly forested landscapes than in fragmented agricultural areas. Ultimately, predation rates should reflect the differences in predator communities associated with different landscape configurations (Andrén 1995). In midwestern and eastern North America and Scandinavia, increased fragmentation and agriculture are often associated with large increases in corvids, raccoons, skunks and squirrels (Andrén 1992, Faaborg et al. 1995). In contrast, in our system, the density of the most abundant nest predator, the Red Squirrel, declined in increasingly fragmented, agricultural landscapes and though Black-billed Magpies increased in these areas, they were never very abundant. Raven and Stellers Jay were detected very rarely on our sites and incidental observations of fox, chipmunks, weasels, raccoons, and skunks were recorded in both landscapes, but their relative abundance has not been quantified. However, Red squirrels are known to be important nest predators in western forest systems (Martin 1993) and the abundance of forest predators such as squirrels, may have a stronger influence on nest predation in western systems than in areas studied in eastern North America.

The lack of patch size or edge effects found in the Bitterroot Valley runs counter to results from studies in eastern North America where historically contiguous habitats have been fragmented by human land use (Gates and Gysel 1978, Chasko and Gates

1982, Brittingham and Temple 1983, Wilcove 1985, Small and Hunter 1988, Yahner 1988, Møller 1989). However, recent work in the Midwest suggests that edge effects are dependant on landscape context (Donovan et al. 1997) and western riparian habitats are linear and patchy by nature; very little of the habitat we studied was more than 150 m from an edge of some kind. Additionally, though patch size varied considerably among sites, patches were not very isolated from other deciduous habitat and most edges were with water and meadows — habitats that may not themselves attract predators. The natural patchiness and lack of isolation both likely contribute to the lack of any consistent edge effect.

Thus habitat fragmentation in the western United States does not necessarily lead to higher predation rates. Though this finding, and the lack of any evidence for increased predation around habitat edges, is different from results from other parts of North America, it is similar to fragmentation effects throughout much of Europe, where predation rates are lower in human settled areas (Martin and Clobert 1996). Fragmentation of hardwood forests in the midwestern United Sates and other formerly contiguous habitats appears to cause an increase in generalist predators that often use habitat edges (Andrén 1992, Robinson et al. 1995, Donovan et al. 1995). This increase must outweigh decreases in forest interior predators, and predation rates rise in fragmented habitats. In western deciduous forests the balance may be shifted, such that the decline of forest predators associated with landscape fragmentation is more pronounced than the increase in generalist predators.

Parasitism

Forest cover has been repeatedly used to predict cowbird abundance and brood parasitism in the midwestern United States (Robinson 1992, Robinson and Wilcove 1994, Robinson et al. 1995, Donovan et al. 1995, 1997). However, our data show that forest cover may not always be a good predictor of parasitism. In the present study, the variables most directly related to the rates of brood parasitism are those directly linked to the life-history of the cowbird: food resources and the density of hosts. Forest cover is only weakly correlated with parasitism pressure on individual species, both in the current study (Fig. 4C-D) and in the Midwest (Robinson et al. 1995) where parasitism on four of eight species studied showed no significant relationships with forest cover. In contrast, human habitation was strongly correlated with parasitism rates in our study. Primary cowbird feeding areas include short-grass fields, livestock corrals, feedlots, and bird-feeders (Rothstein et al. 1984, 1987, Verner and Ritter 1983, Thompson 1994, M. L. Johnson and J. J. Tewksbury, *unpublished data*). All of these areas are associated with human habitation in the Bitterroot Valley, and likely elsewhere in the West. Therefore, the proximity of human habitation, representing feeding areas for cowbirds, may have a greater affect on parasitism than does the percent of a landscape that is forested.

Independent of feeding resources, the cumulative density of hosts also affected parasitism rates. Other studies have shown that cowbirds are more abundant in habitat types with greater cumulative host density (Verner and Ritter 1983, Rothstein et al. 1984, Robinson and Wilcove 1994) but the effect of variance in cumulative host density within a habitat has received little study (but see Barber and Martin 1997). Our results suggest that cowbirds congregate where host density is high and subsequently parasitize a greater proportion of nests (also see Barber and Martin 1997).

Human habitation and host density represent direct links to the foraging and reproductive biology of the cowbird. The strong independent relationships of both these variables with parasitism suggest that cowbirds are attempting to minimize travel distances while maximizing both reproductive opportunities and foraging efficiency. Application of these relationships may allow spatially explicit predictions of parasitism rates over broad landscape scales.

Nesting productivity

The largest demographic impacts faced by most birds on their breeding grounds are nest predation and brood parasitism (Brittingham and Temple 1983, Trail and Baptista 1989, Martin 1992, 1993b, 1996, Pease and Grzybowski 1995, Brawn and Robinson 1996, Woodworth *In press b*). In some landscapes, fragmentation may cause increases in both predators and cowbirds, resulting in large differences in breeding productivity between forested landscapes and fragmented agricultural landscapes (Donovan et al. 1995, Robinson et al. 1995, Brawn and Robinson 1996). However, in the Bitterroot Valley, riparian areas in fragmented landscapes have lower predation rates, but high rates of cowbird parasitism. Thus overall nesting productivity depends on the relative importance of these processes on different species. Non-parasitized species, such as the Cedar Waxwing and American Robin, fledge between 1.4 and 1.5 young per nesting attempt in agricultural landscapes (Fig. 5). Given current estimates of survival (Martin 1995), pairs would need an average of only 2 nesting attempts per season for local recruitment to balance mortality. Riparian habitats in agricultural settings in the Bitterroot Valley thus appear to serve as population sources for these species. In contrast, populations of the same species nesting in forested landscapes may need an average of

3.5 to 4.5 nesting attempts per season to achieve a stable population. American Robins may achieve such levels (Tewksbury, unpublished data), but Cedar Waxwings likely do not and thus these forested areas are likely population sinks for Cedar Waxwings. The large difference in productivity, due to differences in predation rates between landscapes, may cause local source - sink dynamics to occur for some non-parasitized species. For heavily parasitized species, higher parasitism in agricultural areas decreases productivity to levels equal or below productivity in forested areas. Because of high parasitism in fragmented landscapes and high predation in forested areas, Yellow Warblers and Warbling Vireos nesting in either landscape fledge only 0.9 to 1.0 young per attempt. At that fecundity level, Yellow Warblers, which do not raise multiple broods in our system, would need to attempt between 3 and 7 re-nests following nest failure to achieve stable population levels. Warbling Vireos, which commonly raise multiple broods, would need to initiate between 3 and 4 nesting attempts to achieve stable population growth. Clearly, we need better estimates of both adult and juvenile survival to make more precise estimates of population health for these species, but our results indicate that neither landscape type studied in the Bitterroot Valley offer strong source habitat for these species due to the dual affects of predation and parasitism.

Conclusions

Landscape level processes determining predation and parasitism pressure may be more complex than often appreciated. Predation patterns in any landscape depend on the response of different predator species to landscape composition, and the relative effects of these predators on different bird species. Because of the complex nature of these interactions, universal relationships between fragmentation and nest predation are unlikely. However, parasitism pressure may be predicted with a high degree of accuracy by considering those variables that relate directly to the resources used by cowbirds — food and hosts. Because cowbirds use similar types of resources throughout their range, relationships between landscape features and parasitism rates derived in one location may be applicable to many others.

This research illustrates the need for empirical study of the effects of landscape fragmentation on fundamental demographic processes such as nest predation and brood parasitism in landscapes with diverse histories of natural fragmentation. Explicit comparison of historically fragmented habitats with those that have evolved as contiguous habitat may lead to a more holistic understanding of the impacts of human caused fragmentation. By combining this work with examination of predator community response to fragmentation, we may gain a more complex, but perhaps more complete understanding of the effects of habitat fragmentation.

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Literature Cited

Ambuel, B., and S. A. Temple. 1983. Area-dependant changes in bird communities and vegetation of southern Wisconsin forests. Ecology 64:1057-1068.

Andrén, H. 1992. Corvid density and nest predation in relation to forest fragmentation: a landscape perspective. Ecology **73**:794-804.

Andrén, H. 1995. Effects of landscape composition on predation rates at habitat edges. Pages 225-255 *in* L. Hansson, L. L. Fahrig and G. Merriam, editors. Mosaic landscapes and ecological processes. Chapman and Hall, London.

Askins, R. A., J. F. Lynch, and R. Greenberg. 1990. Population declines in migratory birds in eastern North America. Current Ornithology **7**:1-57.

Attiwill, P. M. 1994. The disturbance of forest ecosystems: the ecological basis for conservative management. Forest Ecology and Management **63**:247-300.

Barber, D. R. and T. E. Martin. 1997. Influence of alternate host densities on brown-headed cowbird parasitism rates in black-capped vireos. Condor **99**:595-604.

Bock, C. E., V. A. Saab, T. D. Rich, and D. S. Dobkin. 1993. Effects of livestock grazing on Neotropical migratory landbirds in Western North America. Pages 296-309 *in* D. M. Finch, and P. W. Stangel, editors. Status and management of Neotropical Migratory Birds. U.S. Forest Service Rocky Mountain Forest and Range Experiment Station General Technical Report **RM-229**.

Brawn, J. D., and S. K. Robinson. 1996. Source-sink population dynamics may complicate the interpretation of long-term census data. Ecology **77**:3-12.

Brittingham, M. C. and S. A. Temple. 1983. Have cowbirds caused forest songbirds to decline? Bioscience **33**:31-35.Chasko, G. G. and G. E. Gates 1982. Avian Habitat suitability long a transmission line corridor in an oak-hickory forest region. Wildlife Monographs **82**:1-41.

Dobkin, D. S., and B. A. Wilcox. 1986. Analysis of natural forest fragments: riparian birds in the Toyabe Mountains, Nevada. Pages 293-299 *in* J. Verner, M. L. Morrison, and C. J. Ralph, editors. Wildlife 2000: Modeling Habitat Relationships of Terrestrial Vertebrates. Univ. Wisconsin Press, Madison.

Donovan, T. M., F. R. Thompson III, J. Faaborg, and J. R. Probst. 1995. Reproductive success of migratory birds in habitat sources and sinks. Conservation Biology 9:1380-1395.

Donovan, T. M., P. W. Jones, E. M. Annand, and F. R. Thompson III. 1997. Variation in local-scale edge effects: mechanisms and landscape context. Ecology **78**:2064-2075.

ESRI (Environmental Systems Research Institute, Inc.) 1989. PC Arc Info version 3.4D. 380 New York Street, Redlands, CA 92373-8100.

Faaborg, J., M. Brittingham, T. Donovan, and J. Blake. 1995. Habitat fragmentation in the temperate zone. Pages 357-380. *in* T. E. Martin and D. Finch, editors. Ecology and management of Neotropical migratory birds: a synthesis and review of critical issues. Oxford University Press, New York.

Freemark, K. and B. Collins. 1992. Landscape ecology of birds breeding in temperate forest fragments. Pages. 443-454 *in* J. M. Hagan and D. W. Johnson, editors. Ecology and conservation of Neotropical migrant landbirds. Smithsonian Institute Press.

Gates, J. E., and N. R. Griffen. 1991. Neotropical migrant birds ad edge effects at a forest-stream ecotone. Wilson Bulletin **103**:204-217.

Gates, J. E., and L. W. Gysel. 1978. Avian nest dispersion and fledgling success in field-forest ecotones. Ecology **59**:871-883.

Hansen, P. L., R. D. Pfister, K. Boggs, B. J. Cook, J. Joy, and D. K. Hinckley. 1995. Classification and management of Montana's riparian and wetland sites. Montana forest and conservation Experiment Station. University of Montana miscellaneous publication **No. 54**. Missoula, MT.

Haskell, D. G. 1995. A reevaluation of the effects of forest fragmentation on rates of bird-nest predation. Conservation Biology **9**:1316-1318.

Hejl, S. J. 1992. The importance of landscape patterns to bird diversity: a perspective from the northern Rocky Mountains. Northwest Environmental Journal **8**:119-137.

Hejl, S. J. 1994. Human-induced changes in bird populations in coniferous forest in western North America during the past 100 years. Pages 232-246 *in* J. R. Jehl Jr., and N. K. Johnson, editors. A century of avifaunal change in western North America . Studies in Avian Biology **No. 15**.

Hensler, G. L., and J. D. Nichols. 1981. The Mayfield method of estimating nesting success: a model, estimators and simulation results. Wilson Bulletin **93**:42- 53.

Hines, J. E., & J. R. Sauer. 1989. CONTRAST Program for the analysis of several survival or recovery rate estimates. Patuxent Wildlife Research Center, U.S. Fish & Wildlife Service Laurel, MD.

Howe, R. W. 1984. Local dynamics of bird assemblages in small forest fragments in Australia and North America. Ecology **65**:1585-1601.

Hutto, R. L., S. M. Pletschet, and P. Hendricks. 1986. A fixed radius point count method for nonbreeding and breeding season use. Auk **103**:593-602.

Johnson, D. H. 1979. Estimating nest success: the Mayfield method and an alternative. Auk **96**:651-661.

Johnson, R. R., L. T. Haight, and J. M. Simpson. 1977. Endangered species vs. endangered habitats: a concept. Pages 86-79 *in* R. R. Johnson and D. A. Jones, editors. Importance, preservation, and management of riparian habitat: a symposium. Fort Collins, CO. U.S. Forest Service General Technical Report **RM-43**.

Knopf, F. L. 1985. Significance of riparian vegetation to breeding birds across an altitudinal cline. Pages 105-111 *in* R.R. Johnson, C. D. Ziebell, D. R. Patton, P. F. Ffolliot and R. H. Hamre, editors. Riparian ecosystems and their management: reconciling conflicting uses. U.S. Forest Service General Technical Report **RM-120**.

Knopf, F. L., R. R. Johnson, T. Rich, F. B. Samson, R. C. Szaro. 1988. Conservation of riparian ecosystems in the United States. Wilson Bulletin **100**:272-282.

Martin, T. E. 1987. Artificial nest experiments: affect of nest appearance and type of predators. Condor **89**:925-928.

Martin, T. E. 1992. Breeding productivity considerations: what are the appropriate habitat features for management? Pages 455-473 *in* J. M. Hagan and D. W. Johnston, editors. Ecology and Conservation of Neotropical Migrants, Smithsonian Institution Press.

Martin, T. E. 1993a. Nest predation and nest sites: new perspectives on old patterns. Bioscience **43**:1-18.

Martin, T. E. 1993b. Nest predation among vegetation layers and habitat types: revising the dogmas. American Naturalist **141**:897-913.

Martin, T. E. 1995. Avian life history evolution in relation to nest sites, predation, and food. Ecological Monographs **65**:101-127.

Martin, T. E. 1996. Fitness Costs of resource overlap among coexisting bird species. Nature **380**:338-340.

Martin, T. E. and G. R. Geupel. 1993. Nest-monitoring plots: methods for locating nests and monitoring success. Journal of Field Ornithology **64**:507-519.

Martin, T. E., and J. Clobert. 1996. Nest predation and avian life-history evolution in Europe versus North America: a possible role of humans? American Naturalist **147**:1028-1046.

Martin, T. E., W. Hochachka, C. J. Conway, and J. W. Jenkins 1996. BBIRD field protocol. Montana Cooperative Wildlife Research Unit. University of Montana. Missoula, MT.

Mayfield, H. F. 1961. Nesting success calculated from exposure. Wilson Bulletin **73**:255-261.

Mayfield, H. F. 1975. Suggestions for calculating nest success. Wilson Bulletin **87**:456-466.

McGarigal, K. and B. J. Marks. 1995. FRAGSTATS: spatial pattern analysis program for quantifying landscape structure. U.S. Forest Service General Technical Report **PNW 351.**

Møller, A.P. 1989. Nest site selection across field-woodland ecotones: the effect of nest predation. Oikos **56**:240-246.

Ohmart, R. D. 1994. The effects of human-induced changes on the avifauna of western riparian habitats. Pages 273-285 in J. R. Jehl Jr., and N. K. Johnson, editors. A century of avifaunal change in western North America. Studies in Avian Biology **No. 15**.

Paton, P. W. C. 1994. The effect of edge on avian nest success: how strong is the evidence? Conservation Biology **8**:17-26.

Pease, C. M. and J. A. Grzybowski. 1995. Assessing the consequences of brood parasitism and nest predation on seasonal fecundity in passerine birds. Auk **112**:343-363.

Ratti, J. T. and K. P. Reese. 1988. Preliminary test of the ecological trap hypothesis. Journal of Wildlife Management. **52**:484-491.

Rice, W. R. 1989. Analyzing tables of statistical tests. Evolution **43**:223-225.

Robinson, S. K. 1992. Population dynamics of breeding Neotropical migrants in a fragmented Illinois landscape. Pgs. 408-418 in J. M. Hagan and D. W. Johnson, editors. Ecology and conservation of Neotropical migrant landbirds. Smithsonian Institute Press.

Robinson, S. K., F. R. Thompson, T. M. Donovan, D. R. Whitehead, and J. Faaborg. 1995. Regional forest fragmentation and the nesting success of migratory birds. Science **267**: 1987-1990.

Robinson, S. K., and D. S. Wilcove. 1994. Forest fragmentation in the temperate zone and its effects on migratory songbirds. Pages 233-249 *in* K. Young and M. A. Ramos, editors. The conservation of migratory birds in the Neotropics. Bird Conservation International. Washington DC.

Roper, J. J. 1992. Nest predation experiments with quail eggs: too much to swallow? Oikos **65**:528-530.

Rothstein, S. I., J. Verner, and E. Stevens. 1984. Radio-tracking confirms a unique diurnal pattern of spatial occurrence in the parasitic Brown-headed Cowbird. Ecology **65**:77-88.

Rothstein, S. I., J. Verner, E. Stevens, and L. V. Ritter. 1987. Behavioral differences among sex and age classes and their relation to the efficacy of a control program. Wilson Bulletin **99**:322-327.

SPSS inc. 1996. Advanced statistics 7.0 update. SPSS inc. 444 North Michigan Avenue, Chicago, IL. 60611. USA.

Saab, V.A., and C.R. Groves. 1992. Idaho's migratory landbirds: description, habitats and conservation. Idaho department of Fish and Game Nongame Wildlife Leaflet **No. 10**.

Sauer, J. R., and B. K. Williams. 1989. Generalized procedures for testing hypotheses about survival and recovery rates. Journal of Wildlife Management **53**:137-142.

Small, M. F. and M. L. Hunter. 1988. Forest fragmentation and avian nest predation in forested landscapes. Oecologia **76**:62-64.

Szaro, R. C. 1980. Factors influencing bird populations in southwestern riparian forests. Pages 403-418 *in* M. Degraph, editor. Management of western forests and grasslands for nongame birds. U.S. Forest Service Intermountain Forest and Range Experimental Station General Technical Report **INT-86.**

Temple, S. A. 1986. Predicting impacts of habitat fragmentation on forest birds: a comparison of two models. Pages 301-304 *in* J. Verner, M. L. Morrison, and C J. Ralph, editors. Wildlife 2000: modeling habitat relationships of terrestrial vertebrates. University of Wisconsin Press, Madison, WI.

Thompson, F. R. III. 1994. Temporal and spatial pattern of breeding in Brown-headed cowbirds in the Midwestern United States. Auk **111**:979-990.

Trail, P. W., and L.F. Baptista. 1993. The impact of Brown-headed Cowbird parasitism on populations of Nuttall's White-crowned Sparrow. Conservation Biology **7**:309-315.

Verner, J., M. L. Morrison, and C. J. Ralph, editors. 1986. Wildlife 2000: Modeling Habitat Relationships of Terrestrial Vertebrates. Univ. Wisconsin Press, Madison.

Verner, J. and L. V. Ritter. 1983. Current status of the brown-headed cowbird in the Sierra National Forest. Auk **100**:355-368.

Villard, M. A., K. Freemark, and G. Merriam, 1992. Metapopulation theory and neotropical migrant birds in temperate forests: an empirical investigation. Pages 474-482 *in* J. M. Hagan and D. W. Johnson, editors. Ecology and conservation of neotropical migrant landbirds. Smithsonian Institute Press.

Wilcove, D. S. 1985. Nest predation in forest tracts and the decline of migratory songbirds. Ecology **66**:1211-1214.

Willebrand, T. and V. Marcström. 1988. On the danger of using artificial nests to study predation. Auk **105**:378-379.

Woodworth, B. L. *In press a.* Brood parasitism, nest predation and season-long reproductive success of a tropical island endemic. Condor.

Woodworth, B. L. *In press b.* The invasion of the Shiny Cowbird in the West Indies: modeling the implications for a single-island endemic vireo. Conservation Biology.

Yahner, R. H. 1988. Changes in wildlife communities near edges. Conservation Biology **2**:333- 339.

Zar, J. H. 1984. Biostatistical analysis, second edition. Prentice Hall, Englewood cliffs, New Jersey, USA.

APPENDIX A: Landscape habitat types designated. Indented habitat types are subclasses.

Habitat Type	Description
Residential Structures	All houses and residences
Commercial Structures	All commercial buildings
Industrial Structures	All industrial areas - lumber yards, saw mills
Farm	
Animal Farm (small)	1 - 5 livestock, private farms, 1 corral
Animal Farm (Medium)	5-15 livestock, large private farms, small training facilities, 1 to 3 corrals
Animal Farm (large)	16 + livestock, commercial farms, multiple corrals and livestock feeding areas
Crop Farm	No livestock or livestock feeding areas seen
Agricultural Land	Most agriculture was used both as cropland and pasture, depending on the season, and so these uses were not separated.
Orchard	Apples mostly
Rangeland	All open range, almost exclusively found East of the Bitterroot Valley
Grass Rangeland	Grass-dominated rangeland
Shrub Rangeland	Shrub dominated rangeland
Coniferous Forest	
Forest	Closed canopy coniferous forest
Woodland	Open canopy with patches of grassland

Appendix 1 Continued

Water	Lakes and reservoirs
Deciduous Riparian	All habitats dominated by deciduous species
Mixed Deciduous / Coniferous Riparian	Riparian habitat with near equal portions deciduous and coniferous growth
Recent Burn	recently burned areas (mostly 1994 burns)
Other habitats delineated	Meadow, river, sandbar, cattails

Table 1: Species parasitized by the Brown-headed Cowbird. Primary hosts are species with greater than 15% of their nests parasitized (_). Only prime hosts are used to control for host density. To examine potential bias of including nests found later in the nesting cycle, we compared parasitism rates using all nests to parasitism rates using only nests found before clutch initiation (Whole period). Bias associated with using all nests is minimal for all species (Pearson's $\chi^2 > 0.2$ in all cases). Whole period parasitism rates are not calculated for species with < 10 nests, sample sizes are shown in parentheses.

Species		% Parasitized (# nests[a])		
common name	Latin (scientific) name	All Nests	Whole period	Prime hosts _ = yes
Common Yellowthroat	*Geothlypis trichas*	71 (7)	- (4)	_
Song Sparrow	*Melospiza melodia*	66 (32)	64 (11)	_
Warbling Vireo	*Vireo gilvus*	63 (68)	73 (26)	_
Yellow Warbler	*Dendroica petechia*	61 (131)	63 (57)	_
Solitary Vireo	*Vireo solitarius*	58 (12)	- (6)	_
Veery	*Catharus fuscescens*	40 (10)	- (3)	_
American Redstart	*Setophaga ruticilla*	41 (61)	38 (29)	_
Willow Flycatcher	*Empidonax trailii*	37 (35)	40 (15)	_
Orange-crowned Warbler	*Vermivora celata*	33 (6)	- (2)	_
MacGillivray's Warbler	*Oporornis tolmiei*	32 (19)	- (5)	_
Dusky Flycatcher	*Empidonax wrightii*	24 (76)	27 (48)	_
Dark-eyed Junco	*Junco hyemalis*	6 (17)	- (2)	

Table 1 (cont.)

Red-winged Blackbird	*Agelaius phoeniceus*	5 (37)	- (9)
Chipping Sparrow	*Spizela passerina*	0 (9)	- (4)

Less common host species

Species		% Parasitized (# nests[a])		Prime hosts _ = yes
common name	Latin (scientific) name	All Nests	Whole period	
Red-eyed Vireo	*Vireo olivaceus*	100 (4)	- (2)	_
Lazuli Bunting	*Passerina amoena*	100 (3)	- (0)	_
Audubon's Warbler	*Dendroica coronata*	100 (2)	- (1)	_
Nashville Warbler	*Vermivora ruficapilla*	100 (1)	- (0)	_
Hammond's Flycatcher	*Empidonax hammondii*	67 (3)	- (1)	_

[a] = numbers of nests monitored in which parasitism was known (from 1995 and 1996).

Table 2: Relationship between the abundance of predators and cowbirds on 16 study sites and landscape metrics measured at two spatial extents (1 km and 2 km radius landscapes) around each site. For each test, n = 16, two models were run using type I sums of squares. In the first model, the 1 km extent was forced first, followed by the 2 km extent; in the second model the 2 km extent was forced first. This was done to determine which landscape extent explains a higher proportion of the variance in density among sites (has a higher F) when forced first in the model. Variables entered second act only on variation not explained by the first variable entered. The most relevant extent is highlighted in bold for each species considered.

Landscape Variable	Abundance on sites§	Entered First			Entered Second		
		extent	F	*P*	extent	F	*P*
Forest Cover	Squirrel	**1 km**	**14.2**	**< 0.0005**	2 km	0.1	0.712
		2 km	13.4	0.003	1 km	0.9	0.353
Forest Cover	Magpie	1 km	12.6	0.004	2 km	4.4	0.056
		2 km	**14.6**	**0.002**	1 km	2.3	0.153
Residential development‡	Cowbird	**1 km**	**11.2**	**0.005**	2 km	1.3	0.283
		2 km	9.9	0.008	1 km	0.0	0.987

Table 2 (cont.)

‡ Log transformed

§ from fixed radius point counts.

Table 3: Results from ANCOVA tests for four different edge types. The dependent variable is survival days, site and species are entered as main effects, and distance to edge is a linear covariate. df values are variable as the number of species and nests that were in proximity to different edge types varied. After adjusting for multiple tests, we found no effects of distance to edge on predation rates.

	Edge Type											
	Field			Meadow			Water			Conifer		
Source of variation	df	F	P	df	F	P	df	F	P	df	F	P
Species	10	1.264	0.30	17	1.463	0.12	21	1.214	0.24	17	0.946	0.52
Site	9	0.896	0.54	14	1.974	0.03	10	1.481	0.15	12	1.373	0.19
Distance to edge	1	0.807	0.38	1	1.226	0.27	1	0.309	0.58	1	0.417	0.52
Site x Distance to edge				14	1.298	0.22	9	1.215	0.29	12	0.778	0.67
Species x Distance to edge				17	1.371	0.16						
Error	28			130			238			136		

Table 4: Partial regression coefficients between percent of nests parasitized and patch size, forest cover, and percent human habitation within 1 km of each study site in the Bitterroot Valley in western Montana.† The standardized partial regression coefficient (*B_{st}*), the partial R^2 (R^2_{part}), and the associated *P* measure the effect of one factor after accounting for the effects of the other factors.

Source of variation	B_{st}	R^2_{part}	*P*
patch size	0.03	< 0.01	0.83
forest cover	0.07	0.01	0.78
human habitation	**0.83**	**0.50**	**0.005***

† Data is percent of all nests parasitized for all primary hosts (see table 1) on each study site; n = 16 study sites, 531 nests.

* Significant relationship after Bonferroni adjustment.

Table 5: Nesting parameters for the four most common open-cup nesting species on sites in fragmented agricultural landscapes and unfragmented forested landscapes in the Bitterroot Valley of western Montana. These parameters are used in equation 1 and 2 to generate nesting productivity. The number fledged is calculated for both landscape types combined. Sample sizes are shown in parentheses.

Species Landscape*	Daily nest mortality by cause		NS†	SD‡	SP§	F_{np}∥	(F_{wp})¶
	Predation	Parasitism					
Cedar Waxwing							
Forested	0.0248	0.0	24.9	1.8 (18)			
Agricultural	0.0138	0.0	46.4	2.2 (30)	0.0	2.88 (9)	n/a
American Robin							
Forested	0.0282	0.0	33.7	5.7 (57)			
Agricultural	0.0178	0.0	50.2	4.7 (156)	0.0	2.93 (57)	n/a
Warbling Vireo							
Forested	0.0197	0.0081	32.6	5.1 (55)	11.1 (9)		
						3.1 (10)	2.0 (3)

Table 5 (cont.)

Agricultural	0.0130	0.0130	32.7	4.6 (49)	27.3 (11)		
Yellow Warbler							
Forested	0.0267	0.0067	29.1	9.2 (24)	0.0 (4)		
Agricultural	0.0176	0.0132	35.7	6.1 (266)	50 (38)	3.5 (13)	2.2 (10)

* landscape: Forested = 8 study sites with greater than 50% forest cover in the 1 km landscape surrounding the site, agricultural = 8 study sites with less than 50% forest cover.

† Mayfield adjusted percent of nests successful (Daily nest success raised to the power of the nesting interval).

‡ Maximum likelihood standard deviation for overall nesting success (Johnson 1979).

§ Percent of successful nests that were parasitized.

| Mean number of young fledged from successful non-parasitized nests. Data from all nests in which the exact number fledged is known.

Average number of natal young fledged from successful nests that were parasitized. Success = at least 1 natal young fledged. Data is from all nests in which the exact number fledged is known.

Figure Legends

Fig. 1: The study sites were located in Ravalli county in western Montana. Legend is for B and C. A: Study sites were spread over a 35 mile section of the Bitterroot Valley. White area is agricultural, black is forested, checkered is mixed forest and agriculture. White circles with gray boarders are sites in forested landscapes, gray circles with black boarders are sites in agricultural landscapes. B and C: Landscape features within 1 km of two sites, one forested (B) and one fragmented by agriculture and human development (C). Larger (2 km extent) landscapes were also tested, but found to be less useful in predicting predator and cowbird numbers (see text). All further references to landscape features are at the 1 km scale.

Fig. 2: Daily mortality due to predation for the five open-cup nesting species for which we have sufficient sample size (above error bars) in both forested landscapes, and agricultural landscapes. Error bars are maximum-likelihood estimators. A 2-tailed, paired t-test on mean predation mortality for each species by treatment combination was significant after Bonferroni correction ($t = 6.3$, $df = 4$, $P = 0.003$).

Fig. 3: Mean abundance of Red squirrels and Black-billed Magpies on our study sites (detections per 50 m fixed radius point count), as a function of percent coniferous forest cover on 1 km landscapes. Red Squirrels (A) increased with increasing forest cover, while Black-billed magpies (B) only occurred on sites

with very low coniferous forest cover. ○ = Sites in forested landscapes, ● = Sites in agricultural landscapes.

Fig. 4: Relationship between parasitism rates and percent forest cover. All hosts pooled (A), followed by the two most abundant species considered individually, Yellow Warbler (B) and Warbling Vireo (C). * = significance after Bonferroni correction.

Fig. 5: Partial regression residual plots illustrating the relationship between parasitism rates and human habitation (A, C, E) and host density (B, D, F). Parasitism pressure on all prime cowbird hosts combined (A), Yellow Warbler (C), and Warbling Vireo (E) as a function of percent human habitation while controlling for the density of all potential hosts, and the relationship between the density of all prime hosts and parasitism pressure: on all prime hosts (B), Yellow Warbler (D) and Warbling Vireo (F) while controlling for human habitation. Prime hosts are listed in Table 1. In all three cases, the full models were highly significant. Sample sizes are 531 nests on 16 sites for all hosts; 153 nests on 9 sites for Yellow Warblers and 87 nests on 8 sites Warbling Vireos. B_{st} is the standardized partial regression coefficient. All relationships were significant after controlling for multiple tests.

Fig. 6: Combined impact of nest predation and brood parasitism on the fecundity of two species rarely parasitized by cowbirds and two heavily parasitized species.

The mean number of young fledged per attempt was determined using demographic data from table 5 and equations 1 and 2.

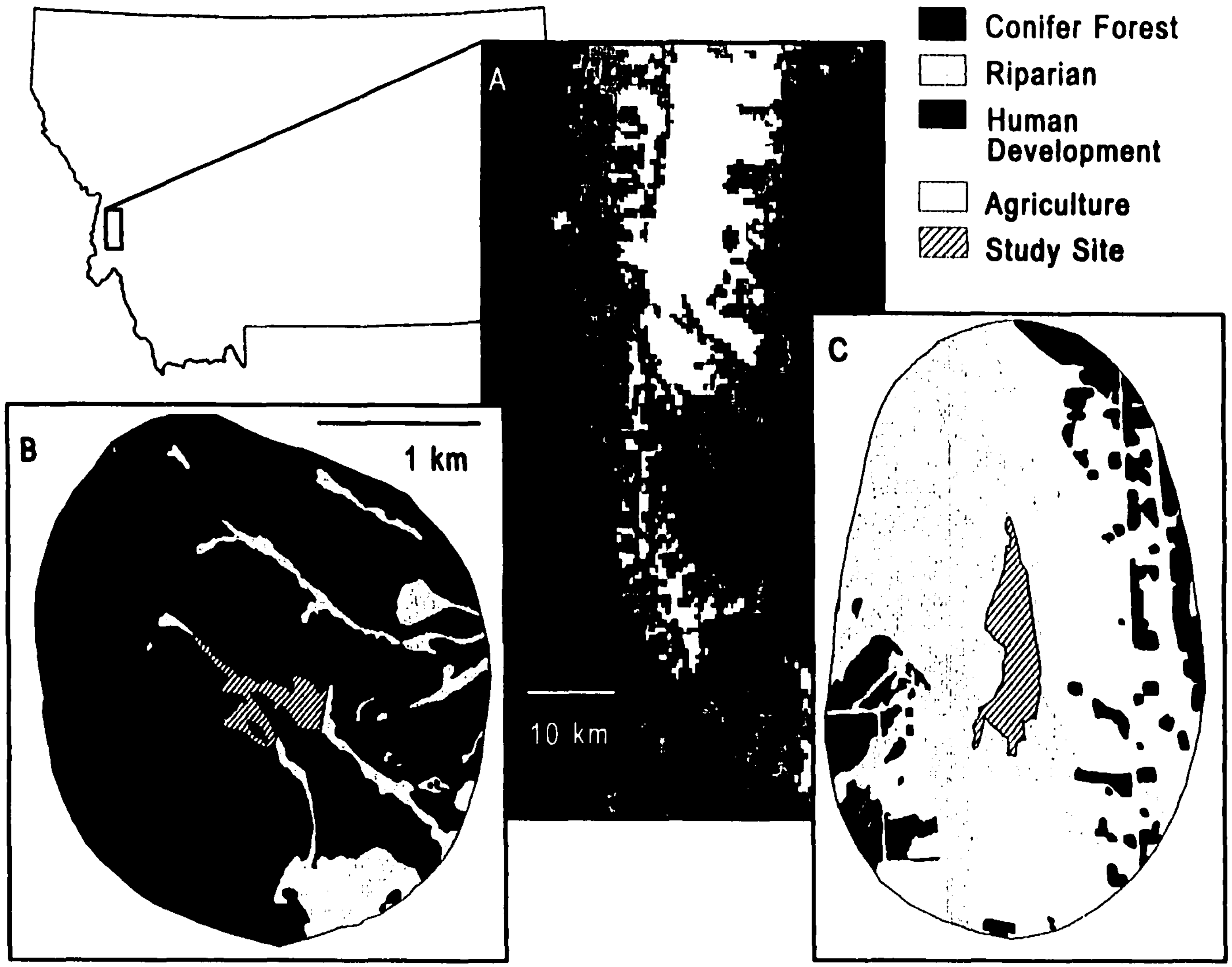
Conifer Forest
Riparian
Human Development
Agriculture
Study Site
A
10 km
B
1 km
C

Figure 1

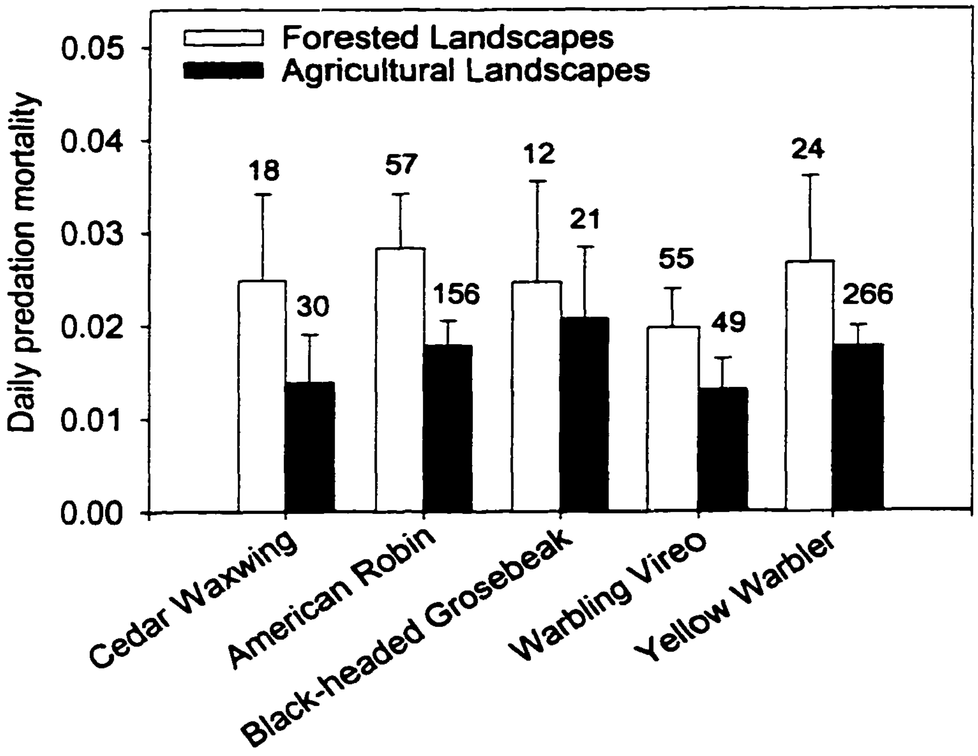
Forested Landscapes
Agricultural Landscapes
Daily predation mortality
0.05
0.04
0.03
0.02
0.01
0.00
18
30
57
156
12
21
55
49
24
266
Cedar Waxwing
American Robin
Black-headed Grosebeak
Warbling Vireo
Yellow Warbler

Figure 2

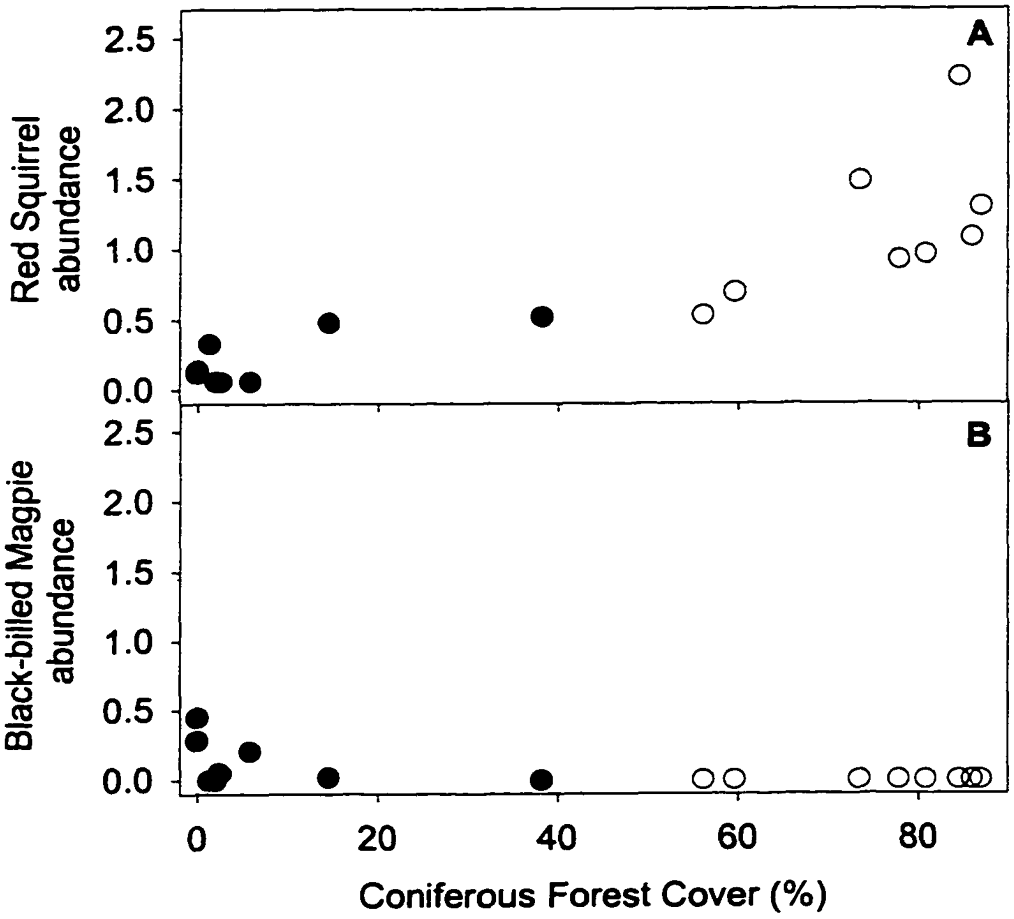
A
B
Red Squirrel abundance
Black-billed Magpie abundance
0.0
0.5
1.0
1.5
2.0
2.5
0
20
40
60
80
Coniferous Forest Cover (%)

Figure 3

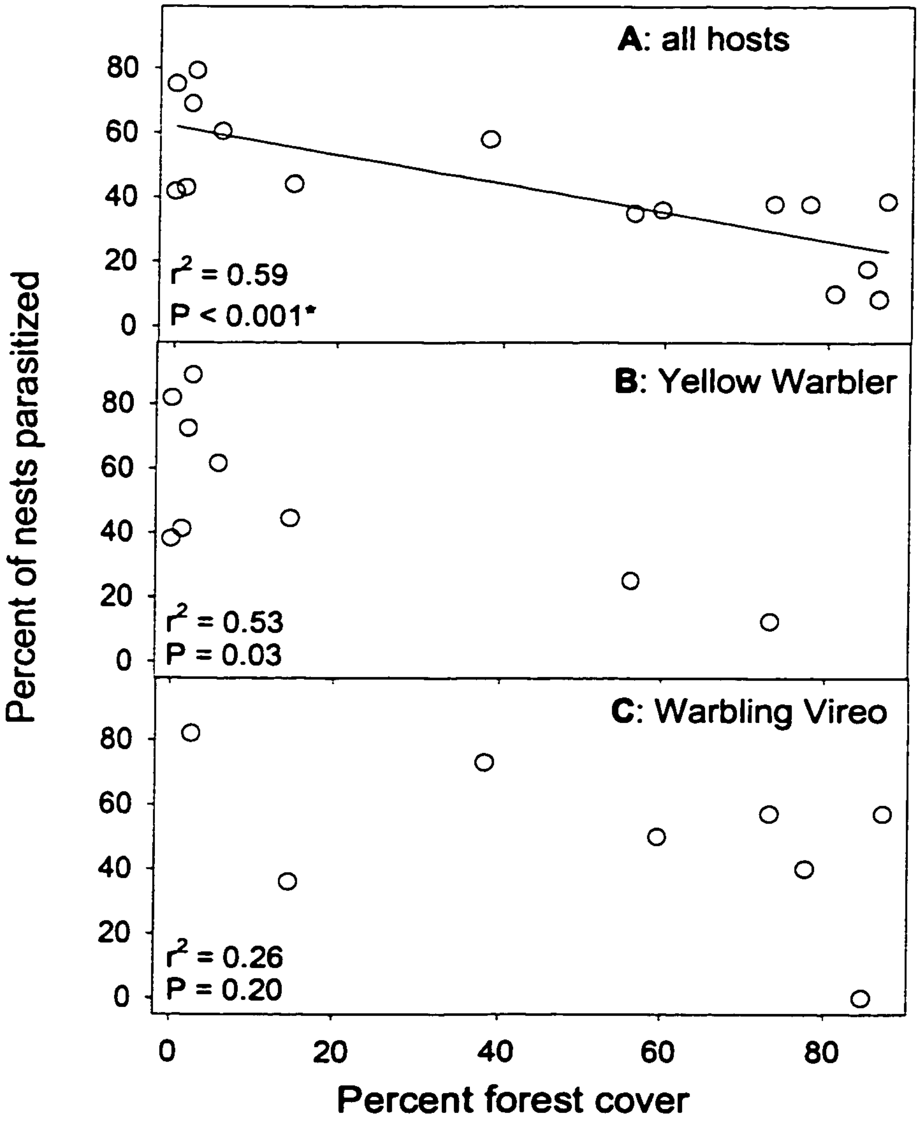
A: all hosts
$r^2 = 0.59$
$P < 0.001^*$
B: Yellow Warbler
$r^2 = 0.53$
$P = 0.03$
C: Warbling Vireo
$r^2 = 0.26$
$P = 0.20$
Percent of nests parasitized
0
20
40
60
80
Percent forest cover

Figure 4

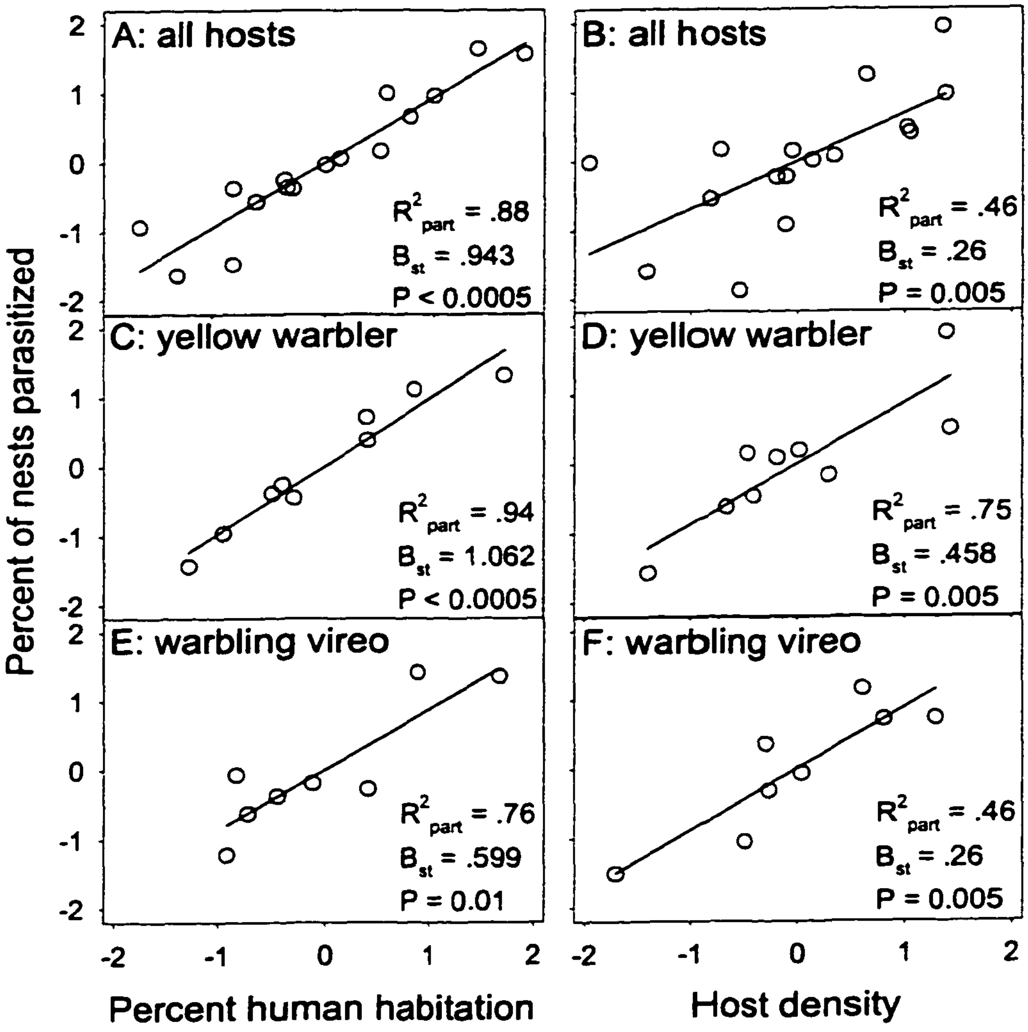
A: all hosts
R^2_{part} = .88
B_{st} = .943
P < 0.0005
B: all hosts
R^2_{part} = .46
B_{st} = .26
P = 0.005
C: yellow warbler
R^2_{part} = .94
B_{st} = 1.062
P < 0.0005
D: yellow warbler
R^2_{part} = .75
B_{st} = .458
P = 0.005
E: warbling vireo
R^2_{part} = .76
B_{st} = .599
P = 0.01
F: warbling vireo
R^2_{part} = .46
B_{st} = .26
P = 0.005
Percent of nests parasitized
2
1
0
-1
-2
-2
-1
0
1
2
Percent human habitation
Host density

Figure 5

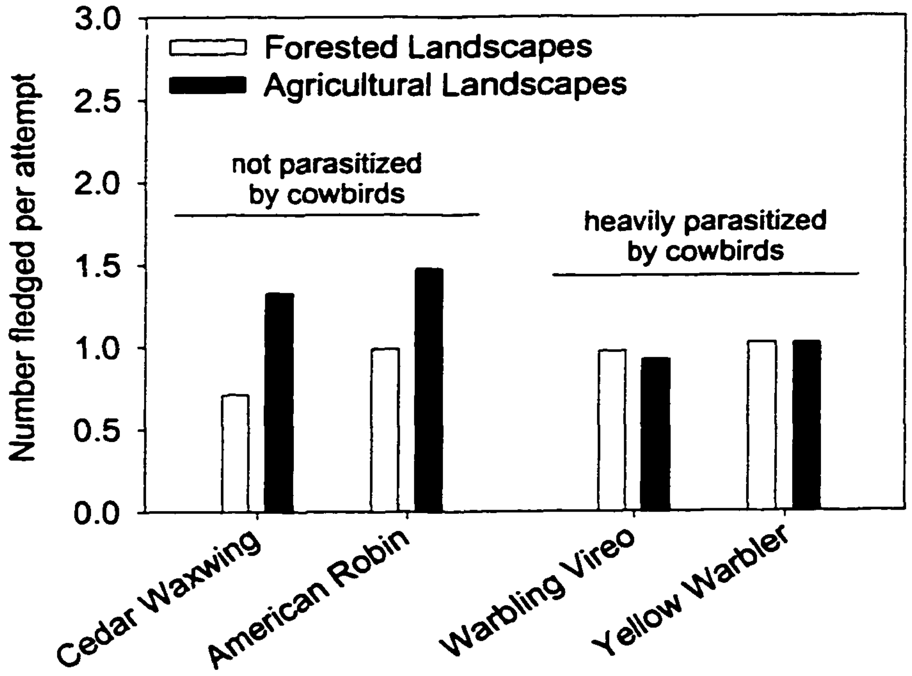
3.0
2.5
2.0
1.5
1.0
0.5
0.0
Number fledged per attempt
Forested Landscapes
Agricultural Landscapes
not parasitized by cowbirds
heavily parasitized by cowbirds
Cedar Waxwing
American Robin
Warbling Vireo
Yellow Warbler

Figure 6

Chapter 2

Cowbirds in a Western Valley: effects of landscape Structure, Vegetation and Host Density

Abstract

Brown-headed Cowbird (*Molothrus ater*) abundance varies dramatically over both large and small spatial scales, causing extreme heterogeneity in parasitism pressure. Understanding the factors responsible for the occurrence and relative abundance of cowbirds is thus essential for properly predicting the regional impact of cowbirds on different host species. We studied the occurrence and relative abundance of Brown-headed Cowbirds (*Molothrus ater)* across three vegetation types in the foothills and valley floor of the Bitterroot Valley in western Montana. Using multiple logistic regression and univariate analyses, we examined the potential impacts of landscape structure, habitat type, distance to agricultural areas, and the density of the cowbird host community on the occurrence and relative abundance of cowbirds. We never encountered cowbirds more than 4 km from agricultural areas, and the distance to large agricultural areas was the strongest predictor of cowbird occurrence and relative abundance. Topographic location of survey points was also important in predicting cowbird occurrence, as cowbirds were almost never encountered within steep-sided canyons. Outside of canyons, both host density and vegetation type appear to influence cowbird abundance, with more cowbirds in deciduous riparian areas and areas of higher host density. Cowbird occurrence and abundance may be mediated by multiple features of the landscape and host community, but in the Bitterroot Valley, cowbird abundance appears greatest in deciduous riparian communities within 2 km of agricultural areas. Intensive research into the demographic impact of cowbirds and the effectiveness of different management options should be directed at species that are confined to these areas for breeding.

Keywords: Brown-headed Cowbirds, *Molothrus ater*, landscape ecology, fragmentation, parasitism pressure, host density.

Introduction

Numerous studies have demonstrated the detrimental impacts of Brown-headed Cowbirds (*Molothrus ater*) on a wide variety of hosts (Nolan 1978, Sedgwick and Knopf 1988, Marvil and Cruz 1989, Trail and Baptista 1993, Greene *this volume*, Whitfield and Sogge *this volume*) and the potential for cowbirds to precipitate the decline and extirpation of some species (Mayfield 1960, 1977; Gaines 1974; Goldwasser et al. 1980; Harris et al. 1987; Franzreb 1989). Given the large impact cowbirds can have on host populations, and the continental range of cowbirds, understanding the landscape features correlated with the distribution of cowbirds is important in identifying habitats and species that are potentially at risk from parasitism (Verner and Ritter 1983; Donovan et al. 1997, in press; Thompson et al. in press).

Due to their parasitic nature and lack of parental care, cowbirds can decouple breeding and feeding behaviors and choose breeding habitats that have the highest density of nests available for parasitism regardless of food availability (Rothstein et al. 1984, Robinson et al. 1995a, Thompson 1994). Cowbirds are constrained to some extent, however, by the distance between breeding and feeding areas (Verner and Ritter 1983, Rothstein et al. 1994, Thompson 1994), and thus the distribution of cowbirds may be strongly dependent on the distribution of breeding and feeding areas on the landscape. Cowbirds have been reported to move as far as 7 to 12 km from breeding areas to feeding locations (Rothstein 1980, 1984, 1987; Thompson 1994; Goguen and Mathews *this volume*), but while a few cowbirds may move long distances, the majority of cowbirds appear to move less than 1.5 km between these areas (Thompson 1994), and the proximity and abundance of feeding habitat are the most often cited variables explaining the presence and abundance of cowbirds on the landscape (Rothstein et al. 1980, 1984; Robinson 1992; Rothstein 1994; Thompson 1994; Robinson et al 1995b; Donovan et al. 1995, 1997, in press; Hejl and Young *this volume*; Young and Hutto *this volume*). However, the presence and abundance of cowbirds may also be influenced by a variety of other variables affecting the quality and quantity of breeding habitat. Vegetation (Rothstein et al. 1984, Rosenburg et al. 1991, Robinson et al. *this volume*), topography (Curson and Mathews *this volume*), and host abundance (Barber and Martin 1997, Tewksbury et al. in press, Robinson et al. *this volume*) may all affect cowbird distribution and abundance. While these variables have been examined separately, few studies have included all these variables to predict the occurrence or relative abundance of cowbirds (but see Young and Hutto *this volume*).

We develop a model for predicting cowbird occurrence in the Bitterroot Valley of western Montana using relative abundance point count sampling and logistic regression. We examine how cowbirds are distributed in relation to agriculture, vegetation, topography, and the density of hosts in this western landscape, compare these relations with eastern and midwestern landscapes, and discuss the implications for the management of western forests.

Methods

Study area and study sites

The study was conducted in the Bitterroot Valley of western Montana. Primary point count locations were originally established in 1994 in conjunction with sixteen nest-monitoring sites (Martin et al. 1996) in deciduous riparian communities. These sites were set in local landscapes that ranged from highly fragmented by agriculture to predominantly forested and unfragmented (Fig. 1). Within each nest monitoring site, we established 2 - 7 point counts for a total of 73 point locations. We stratified these points within each site so that all points were greater than 200m from all other points on the site. All points were located in habitats dominated by deciduous trees and shrubs typical of either the black cottonwood (*Populus trichocarpa*) / red - osier dogwood (*Cornus stolonifera*) community type , the quaking aspen (*Populus tremuloides*) / red - osier dogwood community type, or the mountain alder (*Alnus incana*) community type (Hansen et al. 1995).

To understand the features affecting cowbird abundance at a landscape scale in multiple vegetation types, we established an additional 117 point locations in 14 transects extending from the forest farmland interface into the Selway- Bitterroot Wilderness Area (Fig. 1). This area is predominantly Douglas-fir (*Pseudotsuga menziesii*) and ponderosa pine (*Pinus ponderosa*) forest with numerous streams flowing east from the wilderness area to join the Bitterroot River in the valley floor. Streamside vegetation ranges from coniferous riparian areas dominated by Engelmann spruce (*Picea engelmannii*) and grand fir (*Abies grandis*), to deciduous riparian areas dominated by aspen, alder and willow (*Salix spp.*) We established points in three vegetation types: conifer forest (referred to as xeric conifer), conifer riparian, and deciduous riparian. All points were a minimum of 500 m from neighboring points, and we chose locations within vegetation types at least 50m from the edge of the vegetation type whenever possible (many deciduous riparian areas sampled were too narrow to meet this criterion). We positioned points in an attempt to census all three vegetation types over the full range of distances from agriculture. Deciduous riparian vegetation, however, was concentrated near the valley floor where virtually all of the agriculture is located, and our original points (all in deciduous riparian) were on average closer to agriculture than the points established in transects. This prevented us from establishing a completely balanced design (Fig 1). Census locations varied from 40 to 7,700 m from agriculture, with a mean distance of 2,080 m from agricultural development. The Bitterroot Mountains are dissected by steep-sided canyons, and thus some transect points were located within canyons, while others were on much more open terrain. Because of the large differences in topography between these locations, we noted topographic location (canyon or open topography) and included this in our analysis of cowbird distribution. We identified agricultural land use throughout the Bitterroot Valley using existing Landsat satellite data (Redmond and Prather 1996) and determined the distance of all point-count locations to agricultural areas defined by this data set. This agricultural delineation has a minimum mapping unit of 2 ha and thus depicts only large agricultural areas. While cowbirds may also respond to smaller agricultural units and the presence of farm buildings and bird feeders (Tewksbury et al. in press), if reliable associations between cowbird abundance and distance to agricultural areas can be found at this resolution of landscape structure, it will allow managers to use existing information to predict and manage cowbird populations.

Assessing cowbird and host abundance

For this paper, we use point-count data from 1996 only, as this is the only year in which all points were sampled. Point count locations were censused three times during the season, each count was 10 minutes long, and all birds seen or heard were recorded. We standardized detection effort by using only birds seen or heard within 50 m of the observer (Hutto et al. 1986, Ralph et al. 1995). We recorded vocalizations of males and females separately where possible. Two experienced observers (T.S.R. and F.J.W.) conducted all surveys, switching off transects so that both observers surveyed all locations. We recorded noise level at each point (mostly from streams), determined the level at which noise caused a decline in detections, and excluded results from all high noise censuses. All censuses analyzed were conducted at least ½ -hour after sunrise and before 11:00 A.M..

To examine the effect of relative host density on cowbird abundance, we calculated the average abundance of all hosts at each survey location based on all censuses. A species was considered a host if it was parasitized greater than 15% of the time on our nest-monitoring sites (See Tewksbury et al. in press for parasitism rates and nest monitoring methods) or known to be regularly parasitized by cowbirds elsewhere (Table 1). We included this latter category because we have not determined parasitism rates across species in xeric conifer or mesic conifer forests, but we wanted to include all potential hosts in our calculation of host density across all three habitat types. The complete list of hosts (Table 1) includes two species that were not often parasitized on our deciduous riparian nest-monitoring sites, the Chipping Sparrow (see Table 1 for scientific names of bird species) and Dark-eyed Junco, but neither of these species are very abundant in deciduous riparian areas, and both of these species known to be parasitized elsewhere (Buech 1982, Wolf 1987, Graham 1988, Scott and Lemon 1996). These species were included because they may be parasitized more often in coniferous areas where their abundance relative to other hosts is greater. Though we were unable to find data addressing parasitism rates in the Townsend's Warbler, we included this species in our list of hosts because we have seen adults feeding cowbird fledglings, and virtually all other open-cup nesting *Dendroica* species are common cowbird hosts.

Data analysis

We examined the importance of landscapes, vegetation and host communities on cowbird occurrence using multiple logistic regression. On the subset of locations where cowbirds were detected, we examined the importance of these same factors on the relative abundance of cowbirds. This approach has statistical advantages because it avoids the difficulties of properly characterizing relative abundance when a large percentage of sampling points have zero detections, and may be more biologically meaningful if the factors that influence the presence of a species are different than those that influence density.

We included distance to agriculture, vegetation type, host abundance, and topographic location to predict cowbird occurrence through logistic regression. Our a priori hypothesis considered all of these variables important predictors of cowbird occurrence, and we made no predictions regarding interactions; therefore our primary model includes all variables entered without interactions. We also used a forward stepwise model selection procedure to compare with our a priori model. For forward stepwise selection, we used the likelihood ratio method in SPSS v7.5 (SPSS 1996), which calculates P-values using the likelihood-ratio Chi-square test. Variables are entered into the model based on their improvement to the likelihood of obtaining the observed results. The variable that most significantly improves the probability of obtaining the observed results is added to the model first, and all variables are reevaluated after each step. The entry criteria was P = 0.05.

Stepwise procedures have been criticized as unreliable at properly ranking the importance of variables or finding the most parsimonious model (James and McCulloch 1990). Moreover, the predictive power of any logistic model cannot be assessed without validation using data independent of those used to build the model (Hosemer and Lemeshow 1989). To address these problems and compare the predictive ability of our models, we used a bootstrap procedure to predict the occurrence of cowbirds at locations excluded from data used to create the models. We surveyed 190 locations for the occurrence of cowbirds. Our bootstrap procedure was to run 190 logistic regressions for each model (our primary model, the model chosen by forward stepwise selection, and a full model including all two-way interactions for comparison). In each regression, we left a single location out of the data used to create the model and asked the model created with 189 locations to predict the occurrence of cowbirds on the location left out. The case left out was changed each run, so that in 190 runs, we made independent predictions for each location under the model being bootstrapped. We then compared the predictive ability of our model with that of the forward stepwise model and the full model by comparing the percent of points correctly classified with and without cowbirds using McNemar's test, which tests for differences in response (0 or 1) of individuals or locations tested twice (Sokal and Rohlf 1995). If our a priori model classifies independent cases as well as the forward stepwise and full models, we consider it the best working model to use in predicting cowbirds, as it is simpler than the full model, and avoids the uncertainties of stepwise procedures (James and McCulloch 1990). If the other models are significantly better at classifying cases, we have shown that our a priori model is not sufficient to predict cowbird occurrence accurately , and alternative models will need to be developed.

In all logistic regressions, cowbird occurrence at a location was coded as 1 if any cowbirds were detected within 50m of the observer during any of the censuses at the location, and 0 if no cowbirds were detected. As we excluded surveys where noise at a location prevented accurate detection, some locations include data for less than three visits. To correct for this unequal effort, we weighted logistic regression by the number of visits to each location. We also analyzed the occurrence of female cowbirds separately, but as this metric was correlated with the occurrence of all cowbirds (Spearman's Rank Correlation Coefficient = 0.412, $P < 0.001$), and results from logistic regression were similar, we only present the results from all cowbirds. We used distance to agriculture, topography, vegetation type, host density, and all two-way interactions as potential predictive variables. We checked for correlations between the two continuous variables, distance to agriculture and host density, and found no significant correlations in any combination of habitat type and topographic location (bivariate correlations, all P's > 0.7, except within xeric conifer forests, where $P = 0.112$ in open topography, and $P = 0.186$ in canyon habitats).

To examine the factors affecting cowbird occurrence further, we also present the proportion of locations in which cowbirds were detected by distance from agriculture (1 km categories), host density (< 1 host per point, 1 to 2 hosts, 2 to 3 hosts, etc.), and vegetation type. These data were analyzed using Kruskal-Wallis H tests for two sample tests and Mann-Whitney U for multi-way tests.

Analysis of relative abundance of cowbirds was confined to points where cowbirds were detected and thus is not confounded with the logistic analysis of occurrence. Relative abundance is defined as the number of cowbirds detected per 10-min. survey period averaged over all surveys at a given location. To examine the influence of distance from agriculture on cowbird abundance, we used nonlinear regression though the Curvefit function in Sigmaplot version 4 (SPSS 1997). We also analyzed the effect of host density, vegetation type, and topographic location on cowbird abundance using Kruskal-Wallis and Mann-Whitney U tests. Test statistics reported are for Kruskal-Wallis tests unless otherwise noted.

Results

The distance from the census location to the nearest agricultural area was the strongest, most consistent predictor of cowbird occurrence in all logistic models (Table 2). In open topography cowbirds were detected at more than 80% of all points located within 1 km of agricultural areas, but declined rapidly, with less than 40% occurrence in points 2 to 3 km from agriculture and no cowbirds detected in any points farther than 4 km from agriculture (Fig. 2A). On points where cowbirds were present, relative abundance also declined with increasing distance to agriculture (Fig. 2B). This relationship was fit best by an exponential curve ($R^2 = 0.166$; df = 1, 94; $P < 0.001$).

The topographic location was also a strong predictor of cowbird occurrence; cowbirds were detected in a total of 68% of the 140 open topography locations, and only two of the 50 canyon locations (4%). Some of this difference in occurrence is a function of the location of canyon points, which are rarely close to agriculture due to the topography of the Bitterroot Mountains. Additionally, canyon points had lower host density in all habitat types (Fig. 4). However, topographic location was significant in our primary logistic model without interaction terms, and had a larger influence on cowbird occurrence than host density (Table 2), suggesting a strong independent affect of topographic location on cowbird occurrence. Cowbirds occurred at only two canyon locations, precluding a comparison of mean cowbird abundance between open topography and canyons for points where cowbirds were present.

The affects of vegetation type and host density were difficult to separate. Deciduous riparian areas had the highest host density (Fig. 3; open topography $N = 140$, $df = 2$, $\chi^2 = 21$, $P < 0.001$; canyons $N = 50$, $df = 2$, $\chi^2 = 19$, $P < 0.001$), and whereas cowbird occurrence was not related to vegetation type in canyons (Fig 4A; $N = 50$, $df = 2$, $\chi^2 = 1.1$, $P = 0.57$), in open topography, deciduous areas had higher cowbird occurrence as well (Fig. 4A; $N = 140$, $df = 2$, $\chi^2 = 29.8$, $P < 0.001$). When we considered only locations where cowbirds were detected, the relative abundance of cowbirds was also much higher in deciduous riparian areas than either of the other two vegetation types (Fig. 4B; Mann-Whitney $U = 358$, $N = 95$, $P = 0.005$), but the ratio of cowbirds to hosts did not differ between deciduous riparian areas and xeric conifer forest (Fig. 4C; $N = 95$, $P = 0.873$).

In logistic regression, host density had a slightly stronger affect on cowbird occurrence than vegetation type, but neither variable appears as important as distance from agriculture and topographic location (Table 2). Stepwise selection failed to enter both variables, further suggesting that they explain much of the same variance in cowbird occurrence (Table 2). The interaction between host density and topographic location included in the stepwise model is due to the very low frequency of cowbird occurrence in canyons, regardless of host density, coupled with the strong effect of host density on cowbird occurrence in open topography (Fig. 5A; $N = 140$, $df = 5$, $\chi^2 = 14.1$,

$P = 0.015$). However, the relative abundance of cowbirds at open topography locations was not strongly affected by host density (Fig. 5B; $N = 96$, $df = 5$, $\chi^2 = 4.6$, $P = 0.475$).

Our a priori logistic regression model correctly predicted the occurrence of brown-headed cowbirds in 84.8% of all cases, better than the full model and slightly better than the model chosen by forward stepwise section (Table 3). All models correctly classified locations with cowbirds more often than locations where cowbirds were absent.

Discussion

The distribution of cowbirds across potential breeding sites in the Bitterroot Valley appears to be limited by aspects of breeding-site quality and the distance between breeding and feeding areas. Despite our coarse-grain delineation of agricultural areas in the Bitterroot Valley, the distance to the nearest large agricultural area (>2 ha) was the strongest predictor of cowbird occurrence across the landscape. In the Bitterroot Valley, most agricultural areas are used for pasture and row crops, and the strong relationship with agriculture suggests that cowbird distribution in the Bitterroot Valley is limited by the presence and distribution of largely supplemental food sources supplied by human activities. Rothstein et al. (1980), Verner and Ritter (1983), and Wright (*this volume*) reached a similar conclusion in the Sierra Nevada Mountains, where cowbird numbers declined substantially with increasing distance from pack-stations. Young and Hutto (*this volume*) found a similar relationship between cowbird abundance and agriculture throughout the interior Northwest, and Donovan et al.(in press) and Thompson et al. (in press) found the same relationship in the Midwest.

We found no cowbirds beyond 4 km from agricultural development, and while studies in the Sierra Nevada and the Midwest document cowbirds moving farther than 7 km from feeding areas to breeding areas (Rothstein et al. 1984, Thompson 1994) and greater than 10 km in Texas (Goguen and Mathews *this volume*), the majority of cowbirds studied through radio tracking move less than 2 km (Verner and Ritter 1983, Thompson 1994, Goguen and Mathews *this volume*, Tewksbury and Johnson, unpubl. data). Additionally, where there is an abundance of high-quality breeding habitat close to agricultural areas, such as in the Bitterroot Valley, cowbirds may travel shorter distances from breeding sites to feeding areas. In most of the Bitterroot Valley, the distance from any given feeding area to the nearest riparian area is less than 2 km because of the abundant riparian habitat along the river, and the ratio of breeding habitat to feeding habitat appears high throughout the valley floor. In contrast, Midwestern landscapes are dominated by agriculture and the ratio of breeding habitat to feeding habitat is low, thus cowbirds may be forced to travel further from breeding to feeding areas (Thompson 1994). In general, cowbirds may travel longer distances in areas where breeding habitat is limited and closer breeding habitats are saturated by cowbirds.

A less intuitive feature influencing cowbird distribution was the landscape topography; cowbirds consistently avoided steep-sided canyons. We currently do not have enough information to characterize the overall influence of topography on cowbird occurrence, or to determine whether cowbirds avoid canyons because of dispersal patterns from feeding areas or because of decisions made when selecting laying territories. Host density was consistently lower in canyons than in open topography (Fig. 3), but this cannot explain the almost complete absence of cowbirds in canyons, as deciduous communities in canyons had higher host density than xeric conifer areas in open topography (Fig. 3), and cowbirds were detected at greater than 40% of these xeric conifer locations. However, canyon points were also on average further from agricultural areas. These effects together make it difficult to judge the generality of topographic effects on the occurrence of cowbirds without further study and testing of the current logistic model on an independent data set.

Outside of canyons, cowbird occurrence in the Bitterroot Valley appears to be influenced not only by distance to agriculture, but also the density of potential hosts (Fig. 5). Host density differed predictably among vegetation types (Fig. 3), making it possible for cowbirds to choose areas of high host density reliably simply by choosing deciduous riparian areas (Fig. 4). Close examination of our results, however, suggests that host density and the ease of finding nests are both primary factors driving cowbird occurrence and relative abundance, and that vegetation type may only be important to the extent that it influences these other factors. Host density was higher in deciduous riparian areas than in xeric conifer, but the ratio of cowbirds to hosts was not different between these habitats, suggesting that cowbird abundance is tracking host density among these habitats. In contrast, host density in coniferous riparian areas was equal to host density in xeric conifer forest, but cowbirds were much less common in coniferous riparian areas (Fig. 4). We suggest that both deciduous riparian and xeric conifer forests are relatively easy habitats for cowbirds to find nests in, but the tall densely packed trees characteristic of coniferous riparian areas make it difficult for cowbirds to follow hosts to their nests. Additionally, while the diverse host communities characteristic of deciduous riparian and xeric conifer provide suitable nests for cowbirds in all vegetation layers, more than 35% of all hosts detected in coniferous riparian areas were Townsend's Warblers (Table 1), which nest high in conifers (a mean height of 6.7m was reported by Matsuoka et al. (1997)). Cowbirds appear to parasitize lower nests much more frequently than higher nests (Briskie et al. 1990, Tewksbury unpubl. data); thus Townsend's Warblers may not represent accessible hosts for cowbirds.

Ultimately, if we hold constant the cost of getting to a particular breeding location (e.g., the distance between feeding and breeding areas), the occurrence and abundance of cowbirds should be determined primarily by the density and quality of hosts (Verner and Ritter 1983, Rothstein et al. 1984, Robinson and Wilcove 1994, Barber and Martin 1996, Tewksbury et al. in press), modified by any structural differences between habitats that influence the ease with which cowbirds can find host nests (Robinson et al. *this volume*). Our ability to examine the relationship between cowbird abundance and the quality and quantity of available hosts is limited by our understanding of cowbird-host interactions in different vegetation types. Within a vegetation type, cowbirds parasitize some hosts more often than others, and thus may place greater importance on certain hosts (Barber and Martin 1996, Tewksbury et al. in press). Among vegetation types, the host preference of cowbirds may also change due to differences in the relative abundances of hosts of different quality. Indeed, we may expect cowbirds to switch hosts much like the prey switching of predators (Lawton et al. 1974). A better understanding of host availability and preference in western coniferous forest habitats will allow much greater resolution in predicting the abundance and impact of cowbirds based on attributes of the host community.

Management considerations

Our results clearly indicate that deciduous riparian areas near agricultural lands have higher cowbird abundance than other habitat types (Fig. 4). These areas also support more species of breeding birds than any other habitat type in the western United States (Johnson et al. 1977, Knopf 1985, Knopf et al. 1988, Dobkin and Wilcox 1986, Saab and Groves 1992, Bock et al. 1993, Knopf and Samson 1994). In many western states, Ohmart (1994) has estimated that as much as 95% of this habitat has been altered or destroyed by human activities. Given the importance and status of deciduous riparian habitats in the West, coupled with the threat of cowbird parasitism in these areas, we feel that research and management efforts should focus on these areas. We found at least 22 species of cowbird hosts in deciduous riparian habitats, and 10 of these species were not found in other habitat types (Table 1). These species fall into two broad management categories with regards to parasitism: species that are heavily parasitized throughout their primary habitats in the region, and species that are parasitized in some areas but escape parasitism in others. The Common Yellowthroat, Red-eyed Vireo, Willow Flycatcher, Yellow Warbler, and Veery all appear to breed only in the large deciduous areas. In the Bitterroot Valley, these areas occur almost exclusively near the

Bitterroot River and near agriculture. Detailed studies of the demographic impacts of parasitism should focus on these species, as parasitism pressure on these species may be high throughout their breeding habitat and has the potential to cause regional population declines. In contrast, species such as MacGillivray's Warbler and Warbling Vireo, though heavily parasitized in areas near agriculture, also breed in smaller riparian areas far from agriculture. Though breeding success in these areas has not been sufficiently studied, smaller deciduous riparian areas far from agriculture likely provide escape from cowbird parasitism. For these species, the creation and maintenance of healthy deciduous communities buffered from cowbird feeding areas may be the best way to insure stable populations. Currently, however, deciduous riparian habitat has diminished substantially on the Bitterroot National Forest due to effective fire suppression over the past 50 to 60 years (McCune 1982). Management action that reintroduces natural disturbance to these forests and promotes deciduous communities within the forest matrix may protect many host species from population declines due to parasitism.

Although we have identified correlates of cowbird abundance in the Bitterroot Valley, before we can safely extrapolate findings based on cowbird occurrence and relative abundance to parasitism rates, we need to examine the strength of the relationship between point-count data and parasitism (Thompson et al. in press). If the abundance or occurrence of cowbirds on a landscape can be used to index parasitism rates accurately, point-counts can be used as an important tool in directing management, but if these relationships are weak, or vary significantly by habitat, census data can only be used as a qualitative guide in directing more detailed research.

Effective management of cowbirds will require a detailed understanding of the relationships between landscapes and cowbird numbers, and between cowbird numbers and parasitism rates. The specifics of these relationships are unlikely to be constant throughout the range of the cowbird, as differences in host populations, habitat types, topographic features and landscape patterns may all change the density and movements of cowbirds and the impact of cowbirds on host populations. Yet cowbirds may react to these changes in predictable ways throughout their range, and our understanding of the nature of these relationships in one location should help guide research and management in others.

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Literature Cited

Barber, D. R., and T. E. Martin. 1997. Influence of alternate host densities on brown-headed cowbird parasitism rates in black-capped vireos. Condor 99:595-604.

Bock, C. E., V. A. Saab, T. D. Rich, and D. S. Dobkin. 1993. Effects of livestock grazing on neotropical migratory landbirds in Western North America. Pp. 296-309 *in* D. M. Finch, and P. W. Stangel (editors). Status and management of Neotropical migratory birds. USDA Forest Service Gen. Tech. Rep. RM-229. USDA Forest Service, Rocky Mountain Forest and Range Experimental Station, Fort Collins, CO.

Briskie, J. V., S. G. Sealy, and K. A. Hobson. 1990. Differential parasitism of least flycatchers and yellow warblers by the brown-headed cowbird. Behavioral Ecology and Sociobiology 27:403-410.

Buech, R. R. 1982. Nesting ecology and cowbird parasitism of clay-colored, chipping, and field sparrows in a Christmas tree plantation. Journal of Field Ornithology 53:363-369.

Dobkin, D. S., and B. A. Wilcox. 1986. Analysis of natural forest fragments: riparian birds in the Toyabe Mountains, Nevada. Pages 293-299 *in* J. Verner, M. L.

Morrison, and C. J. Ralph (editors). Wildlife 2000: Modeling habitat relationships of terrestrial vertebrates. University of Wisconsin Press, Madison, WI.

Donovan, T. M., P. W. Jones, E. M. Annand, and F. R. Thompson, III. 1997. Variation in local-scale edge effects: mechanisms and landscape context. Ecology 78:2064-2075.

Donovan, T. M., F. R. Thompson, III, J. Faaborg. In press. Cowbird distribution at different scales of fragmentation: tradeoffs between breeding and feeding opportunities, *in* T. Cook, S. K. Robinson, S. I Rothstein, S. G. Sealy, and J. N. M. Smith (editors) Ecology and Management of Cowbirds. University of Texas Press, Austin, TX.

Franzreb, K. E. 1989. Ecology and conservation of the Least Bell's Vireo (*Vireo bellii pusillus*) in California. Western Birds 18:43-49

Gaines, D. 1974. A new look at the nesting riparian avifauna of the Sacramento Valley, California. Western Birds 5:61-80

Goldwasser, S., D. Gaines, and S. Wilbur. 1980. The Least Bell's Vireo in California: a de facto endangered race. American Birds 34:742-745.

Graham, D. S. 1988. Responses of five host species to cowbird parasitism. Condor 90:588-591.

Hansen, P. L., R. D. Pfister, K. Boggs, B. J. Cook, J. Joy, and D. K. Hinckley. 1995. Classification and management of Montana's riparian and wetland sites. Montana

Forest and Conservation Experiment Station. Miscellaneous Publication No. 54. University of Montana, Missoula, MT.

Harris, J. H., S. D. Sanders, and M. A. Flett. 1987. Willow Flycatcher surveys in the Sierra Nevada. Western Birds 18:27-36.

Hosemer and Lemeshow. 1989. Applied logistic regression. John Wiley and Sons, New York, NY.

Hutto, R. L., S. M. Pletschet, and P. Hendricks. 1986. A fixed radius point count method for nonbreeding and breeding season use. Auk 103:593-602.

James, F. R., and C. E. McCulloch. 1990. Multivariate analysis in ecology and systematics: panacea or pandora's box. Annual Review of Ecology and Systematics 21:129-166.

Johnson, R. R., L. T. Height, and J. M. Simpson. 1977. Endangered species vs. endangered habitats: a concept. Pp. 68-79 *in* R. R. Johnson and D. A. Jones (technical coordinators). Importance, preservation and management of riparian habitat: a symposium. USDA Forest Service Gen. Tech. Rep. RM-166. USDA Forest Service, Rocky Mountain Forest and Range Experiment Station, Fort Collins, CO.

Knopf, F. L. 1985. Significance of riparian vegetation to breeding birds across an altitudinal cline. Pp. 105-111 *in* R.R. Johnson, C. D. Ziebell, D. R. Patton, P. F. Ffolliot and R. H. Hamre (editors). Riparian ecosystems and their management: reconciling conflicting uses. USDA Forest Service Gen. Tech. Rep. RM-120. USDA Forest Service, Fort Collins, CO.

Knopf, F. L., R. R. Johnson, T. Rich, F. B. Samson, R. C. Szaro. 1988. Conservation of riparian ecosystems in the United States. Wilson Bulletin 100:272-282.

Knopf, F. L., and F. B. Samson. 1994. Scale perspectives on avian diversity in western riparian ecosystems. Conservation Biology 8:669-676.

Lawton, J. H., J. R. Beddington, and R. Bonser. 1974. Switching in invertebrate predators. Pp. 141-158 *in* M. B. Usher and M. H. Williamson (editors). Ecological stability. Chapman and Hall, London, UK.

Martin, T. E., W. Hochachka, C. J. Conway, and J. W. Jenkins, 1996. BBIRD field protocol. Montana Cooperative Wildlife Research Unit. University of Montana, Missoula, MT.

Marvil, R. E., and A. Cruz. 1989. Impact of Brown-headed Cowbird parasitism on the reproductive success of the Solitary Vireo. Auk 106:476-480.

Matsuoka, S. M., C. M. Handel, and D. D. Roby. 1997. Nesting ecology of Townsend's warblers in relation to habitat characteristics in a mature boreal forest. Condor 99:271-281.

Mayfield, H. F. 1960. The Kirkland's Warbler. Cranbrook Institute, Bloomfield Hills, MI.

Mayfield, H. F. 1977. Brown-headed cowbird: agent of extermination? American Birds 31:107-113.

McCune, B. 1983. Fire frequency reduced two orders of magnitude in the Bitterroot Canyons, Montana. Canadian Journal of Forest Research 13:212-218.

Nolan, V., Jr. 1978. The ecology and behavior of the Prairie Warbler *Dendroica discolor*. Ornithological Monographs No. 26. American Ornithologists Union, Washington, DC.

Ohmart, R. D. 1994. The effects of human-induced changes on the avifauna of western riparian habitats. Studies in Avian Biology No 15:273-285.

Ralph, C. J., J. R. Sauer, and S. Droege (Technical editors). 1995. Monitoring bird populations by point counts. USDA Forest Service Gen. Tech. Rep. PSW-GTR-149. USDA Forest Service Pacific Southwest Forest and Range Experiment Station, Berkeley, CA.

Redmond, R. L., and M. L. Prather. 1996. Mapping existing vegetation and land cover across western Montana and northern Idaho. Executive summary. Wildlife Spatial Analysis Lab, Montana Cooperative Wildlife Research Unit. University of Montana, Missoula, MT.

Robinson, S. K. 1992. Population dynamics of breeding Neotropical migrants in a fragmented Illinois landscape. Pp. 408-418 *in* J. M. Hagan ad D. W. Johnson (editors). Ecology and conservation of Neotropical migrant landbirds. Smithsonian Institute Press, Washington, DC.

Robinson, S. K., and D. S. Wilcove. 1994. Forest fragmentation in the temperate zone and its effects on migratory songbirds. Bird Conservation International 4:233-249.

Robinson, S. K., S. I. Rothstein, M. C. Brittingham, L. J. Petit, and J. A. Grzybowski. 1995a. Ecology and behavior of cowbirds and their impact on host populations.

Pp 428-460 *in* T. E. Martin and D. M. Finch (editors). Ecology and management of Neotropical migratory birds: a synthesis and review of critical issues. Oxford University Press, New York, NY.

Robinson, S. K., F. R. Thompson, T. M. Donovan, D. R. Whitehead, and J. Faaborg. 1995b. Regional forest fragmentation and the nesting success of migratory birds. Science 267: 1987-1990.

Rosenburg, K. V., R. D. Ohmart, W. C. Hunter, and B. W. Anderson. 1991. Birds of the Lower Colorado River Valley. University of Arizona Press, Tucson, AZ.

Rothstein , S. I., J. Verner, and E. Stevens. 1980. Range expansion and diurnal changes in dispersion of the Brown-headed Cowbird in the Sierra Nevada. Auk 97:253-267.

Rothstein, S. I., J. Verner, and E. Stevens. 1984. Radio-tracking confirms a unique diurnal pattern of spatial occurrence in the parasitic Brown-headed Cowbird. Ecology 65:77-88.

Rothstein, S. I., J. Verner, E. Stevens, and L. V. Ritter. 1987. Behavioral differences among sex and age classes and their relation to the efficacy of a control program. Wilson Bulletin 99:322-327.

Rothstein, S. I. 1994. The cowbird's invasion of the Far West: history, causes and consequences experienced by host species. Studies in Avian Biology no. 15:301-315

Scott, D. M, and R. E. Lemon. 1996. Differential reproductive success of brown-headed cowbirds with Northern Cardinals and three other hosts. Condor 98:259-271.

Sedgwick, J. A., and F. L. Knopf. 1988. A high incidence of Brown-headed Cowbird parasitism of Willow Flycatchers. Condor 90:253-256.

Sokal, R. A. and F. J. Rohlf. 1995. Biometry. W. H. Freeman and Company. New York, NY.

SPSS 1997. Sigmaplot 4.0 for Windows Users Manual. SPSS Inc., 444 North Michigan Avenue, Chicago, IL 60611 USA.

SPSS 1996. Advanced statistics 7.0 update. SPSS Inc., 444 North Michigan Avenue, Chicago, IL 60611 USA.

Tewksbury, J. J., S. J. Hejl, and T. E. Martin. In press. Habitat fragmentation in a western landscape: breeding productivity does not decline with increasing fragmentation. Ecology.

Thompson, F. R., III. 1994. Temporal and spatial pattern of breeding in Brown-headed Cowbirds in the Midwestern United States. Auk 111:979-990.

Trail, P. W., and L.F. Baptista. 1993. The impact of Brown-headed Cowbird parasitism on populations of Nuttall's White-crowned Sparrow. Conservation Biology 7:309-315.

Verner, J., and L. V. Ritter. 1983. Current status of the Brown-headed Cowbird in the Sierra National Forest. Auk 100:355-368.

Wolf, L. 1987. Host-parasite interactions of Brown-headed Cowbirds and Dark-eyed Juncos in Virginia. Wilson Bulletin 99:338-350.

Table 1: Relative abundance of Brown-headed Cowbirds and all species included as cowbird hosts in three habitats and two topographic locations, Bitterroot Valley, MT, 1996. Relative abundances are detections within 50 m per 10 minute census period.

		Coniferous Riparian		Xeric Conifer		Deciduous Riparian	
	Topography:	Open	Canyon	Open	Canyon	Open	Canyon
	# of census locations:	9	18	33	19	98	13
Brown-headed Cowbird	*Molothrus ater*	0.037	0	0.283	0.035	0.862	0.026
Willow Flycatcher	*Empidonax trailii*	0	0	0	0	0.061	0
Least Flycatcher	*Empidonax minimus*	0	0	0	0	0.003	0
Hammond's Flycatcher	*Empidonax hammondii*	0.148	0.056	0.293	0.105	0.122	0.231
Dusky Flycatcher	*Empidonax wrightii*	0.074	0	0.061	0.017	0.264	0.115
Veery	*Catharus fuscescens*	0	0	0	0	0.124	0
Swainson's Thrush	*Catharus ustuatus*	0.259	0.398	0.167	0.158	0.151	0.385

Table 1 (cont.)

Solitary Vireo	*Vireo solitarius*	0	0	0.212	0.035	0.092	0.09
Red-eyed Vireo	*Vireo olivaceus*	0	0	0	0	0.032	0
Warbling Vireo	*Vireo gilvus*	0.185	0.139	0.05	0.053	0.541	0.410
Orange-crowned Warbler	*Vermivora celata*	0	0	0.03	0	0.121	0.064
Nashville Warbler	*Vermivora ruficapilla*	0	0	0	0.017	0.012	0
Yellow Warbler	*Dendroica petechia*	0	0	0.010	0	0.599	0.026
Yellow-rumped Warbler	*Dendroica coronata*	0.037	0.102	0.263	0.184	0.08	0.051
Townsend's Warbler	*Dendroica townsendi*	0.741	0.62	0.227	0.263	0.056	0.731
American Redstart	*Setophaga ruticila*	0	0	0	0	0.179	0
Northern Waterthrush	*Seiurus noveboracensis*	0	0	0	0	0.107	0
MacGillivray's Warbler	*Oporornis tolmiei*	0.333	0.083	0.071	0.07	0.360	0.538
Common Yellowthroat	*Geothlypis trichas*	0	0	0	0	0.059	0
Song Sparrow	*Melospiza melodia*	0	0	0	0	0.124	0

Table 1 (cont.)

Dark-eyed Junco	*Junco hyemalis*	0.148	0.028	0.359	0.105	0.082	0.064
Lazuli Bunting	*Passerina amoena*	0	0	0	0	0.005	0

Table 2: Logistic regression models: Results of the primary model, which included all main effects but no interactions, the model generated through forward stepwise selection, and the full model with interactions are presented.

	B^b	SE	Exp $(B)^b$	r^c	P
PRIMARY MODEL: $\chi^2 = 125$, $P < 0.001$ [a]					
Distance to agriculture (m)	-0.0008	0.0002	0.999	-0.2448	> 0.00005
Topographic location[d]	2.0865	0.7946	8.057	0.1365	0.0086
Vegetation type[c]				0.0374	0.1126
Deciduous riparian[e]	2.2094	1.1038	9.110	0.0874	0.0453
Xeric conifer[c]	1.6760	1.1068	5.344	0.0334	0.1300
Host density	0.2911	0.1766	1.338	0.0522	0.0994
Constant	-2.7848	1.3549			0.0398
FORWARD STEP-WISE MODEL $\chi^2 = 119$, $P < 0.001$ [a]					
Distance to agriculture (m)	-0.0008	0.0002	0.999	-0.2414	< 0.00005

Table 2 (cont.)

Vegetation type[c] x Topographic location[d]				0.2381	0.0001
Deciduous riparian x Topographic location[d]	2.9549	0.6860	19.201	0.2510	< 0.00005
Constant	-0.5784	0.7229			0.4233
FULL MODEL $\chi^2 = 127$, $P < 0.001$[a]					
Distance to agriculture	-0.0016	0.0018	0.998	0.0000	0.3753
Topographic location[d]	5.9436	18.4935	381.292	0.0000	0.7479
Vegetation type[c]				0.0000	0.9254
Deciduous riparian[c]	7.3160	18.5851	1504.178	0.0000	0.6938
Xeric conifer[c]	7.2171	18.4377	1362.466	0.0000	0.6955
Host density	-0.2946	1.8471	0.745	0.0000	0.8733
Vegetation type[c] x Host density				0.0000	0.5543
Deciduous riparian[c] x Host density	0.0020	1.4145	1.002	0.0000	0.9988

Table 2 (cont.)

	B^{b}	SE	Exp (B)^{b}	r^{c}	P
Xeric conifer^{c} x Host density	-0.4829	1.4488	0.617	0.0000	0.7389
Topographic location^{d} x Host density	0.6527	1.0136	1.921	0.0000	0.5196
Distance to agriculture by Host density	5.57 E-05	0.0002	1.000	0.0000	0.9279
Vegetation type^{c} x Topographic location^{d}				0.0000	0.8239
Deciduous riparian^{c} x Topographic location^{d}	-6.4737	18.8693	0.002	0.0000	0.7291
Xeric conifer^{c} x Topographic location^{d}	-5.1432	18.5290	0.006	0.0000	0.7813
Distance to agriculture by Vegetation type^{c}				0.0000	0.7316
Distance to agriculture x Deciduous riparian^{c}	0.0005	0.0016	1.001	0.0000	0.7392
Distance to agriculture x Xeric conifer^{c}	0.0001	0.0017	1.000	0.0000	0.9329
Distance to agriculture x Topographic location^{d}	0.0003	0.0008	1.000	0.0000	0.7171

[a] Model χ^2 measures the difference between the likelihood of obtaining the observed results under the final model and the null model without any variables included.

Table 2 (cont.)

[b] B is the regression coefficient for each effect, representing the change in the log odds of cowbird detection with a one unit change in the independent variable. Exp (B) represents the change in actual odds of cowbird occurrence with a one unit change in the independent variable. Odds are defined as the ratio of the probability that an event will occur to the probability that it will not (SPSS 1996).

[c] Correlation between the independent variable and the probability of cowbird occurrence.

[d] Canyon topography is the reference category. Coefficient (B) and Exp (B) for topographic location refers to the increase in the probability of encountering a cowbird in open topography over canyons

[e] Coniferous riparian is the reference category. All coefficients for deciduous riparian and xeric conifer represent the change in probability of encountering a cowbird in these vegetation types when compared to coniferous riparian areas.

Table 3: Bootstrap results. Each model was bootstrapped 190 times with one location left out for independent classification.

	percent of locations classified correctly			
model	without cowbirds	with cowbirds	overall	P[a]
Primary model	78.9%	90.1%	84.8%	
Forward Stepwise Model	79.3%	89.8%	84.7%	0.137
Full Model	75%	89.8%	82.6%	0.063

[a] Two-tailed McNemar test for difference in predictive power between primary model and other models.

Figure legends

Fig. 1: Study site locations and general agricultural land use in the Bitterroot Valley. Large dark gray points are nest searching plots were parasitism rates were monitored, smaller points are census locations in the three habitat types, deciduous riparian areas (triangles), coniferous riparian areas (squares) and xeric conifer forest (circles). Agricultural land (light gray) is from Landsat Image Data.

Fig. 2: Proportion of all census points where cowbirds were detected (+/- 1 maximum-likelihood standard error) in open topography and canyon points as a function of distance from agricultural development (A). Samples sizes (in parentheses), are the number of point locations surveyed; for points where cowbirds were detected, the mean number of cowbirds detected per 10 min. survey (B). As cowbirds were only encountered at two canyon points, data presented are for open topography. The regression line follows an exponential fit (see RESULTS).

Fig. 3: The relationship between the proportion of sites where cowbirds were detected (+/- 1 maximum-likelihood standard error) and the relative density of suitable hosts in open topography and canyons (A). Host density is defined as the number of hosts detected within 50 m of the observer per 10 min survey period. Where cowbirds are present, their relative abundance as a function of relative

host density in open topography (B). See Table 2 for list of all species included in host density calculations and their relative abundances.

Fig. 4: Density of all hosts (mean +/- 1 SE) by habitat type and topographic location.

Fig. 5: Cowbird occurrence (mean +/- 1 maximum-likelihood standard error) in the three vegetation types (sample sizes are the same as figure 4) in both open topography and canyon locations (A). For all survey locations where cowbirds were detected, the mean number of cowbirds detected per 10 min. census (B), and the ratio of cowbirds to hosts in the three vegetation types (C) using only points where cowbirds were detected. Sample sizes for B and C are the same, and are shown in parentheses (B). The ratio of cowbirds to hosts had a strongly left-skewed distribution in deciduous riparian habitats (C), thus the median (solid line) may best represent the distribution. The mean is also shown (dotted line), and boxes are 25th and 75th percentiles, whisker are 10th and 95th percentiles, and points shown are beyond the 10th and 90th percentiles. Cowbirds were detected in only one mesic conifer point (ratio shown as dot in C), and thus our tests for differences between habitat types in cowbird relative abundance and cowbird to host ratio were only between xeric conifer and deciduous riparian habitats.

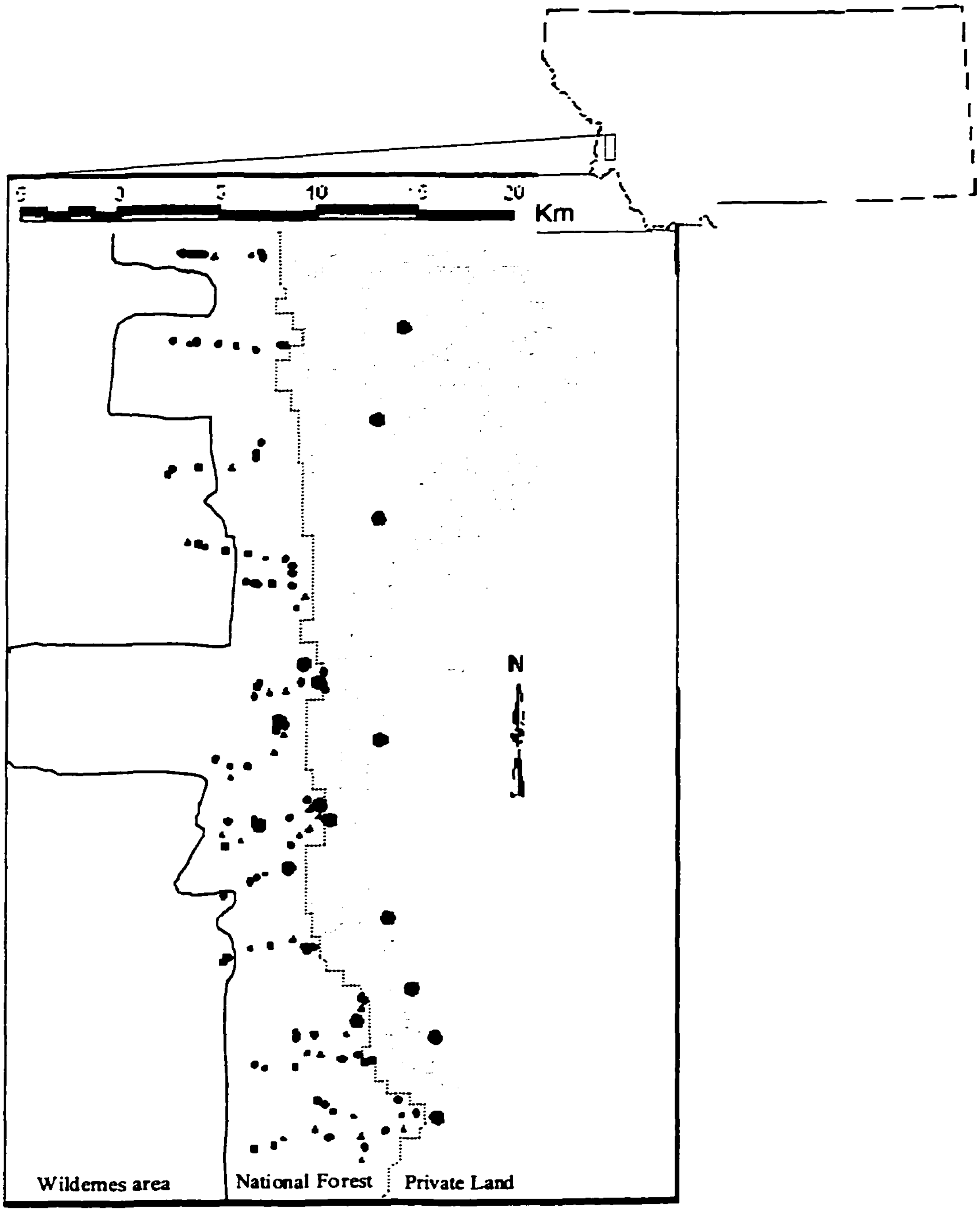

Figure 1

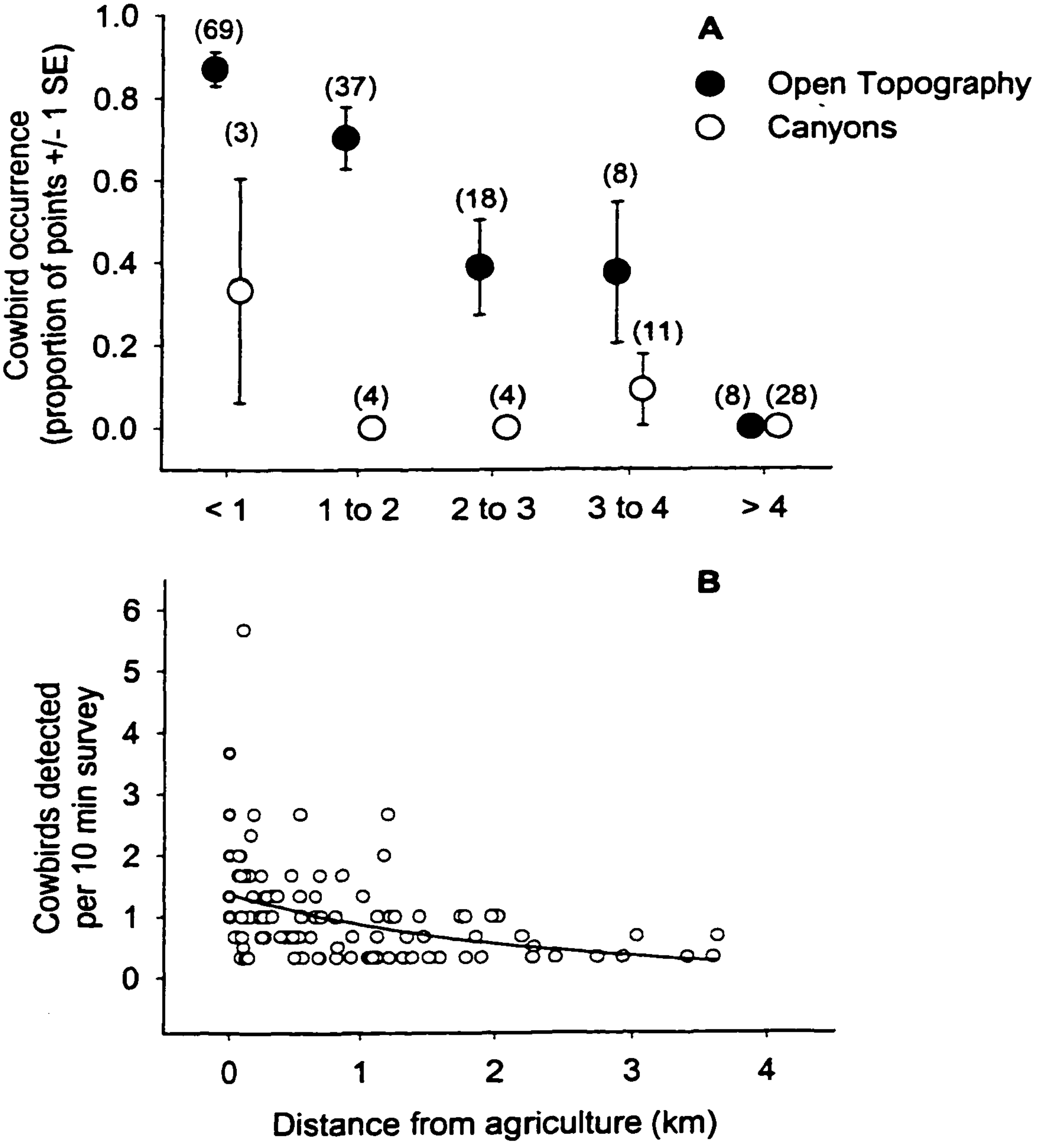
A
Open Topography
Canyons
Cowbird occurrence (proportion of points +/- 1 SE)
1.0
0.8
0.6
0.4
0.2
0.0
(69)
(3)
(37)
(4)
(18)
(4)
(8)
(11)
(8)
(28)
< 1
1 to 2
2 to 3
3 to 4
> 4
B
Cowbirds detected per 10 min survey
6
5
4
3
2
1
0
0
1
2
3
4
Distance from agriculture (km)

Figure 2

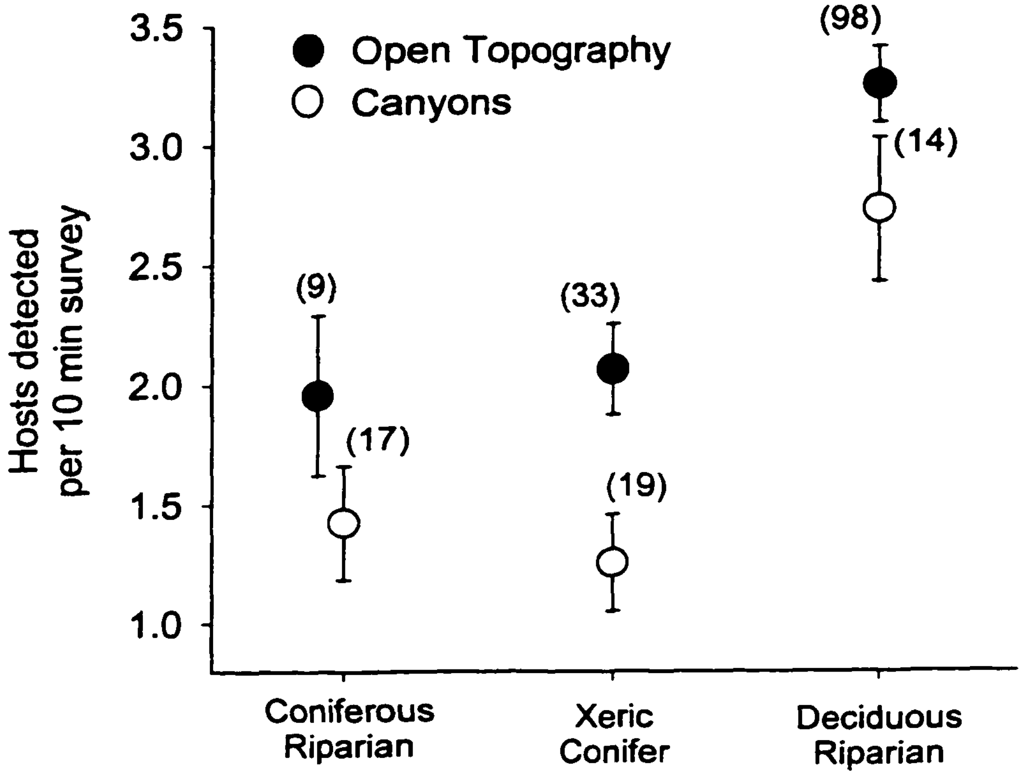
3.5
3.0
2.5
2.0
1.5
1.0
Hosts detected per 10 min survey
● Open Topography
○ Canyons
(9)
(17)
(33)
(19)
(98)
(14)
Coniferous Riparian
Xeric Conifer
Deciduous Riparian

Figure 3

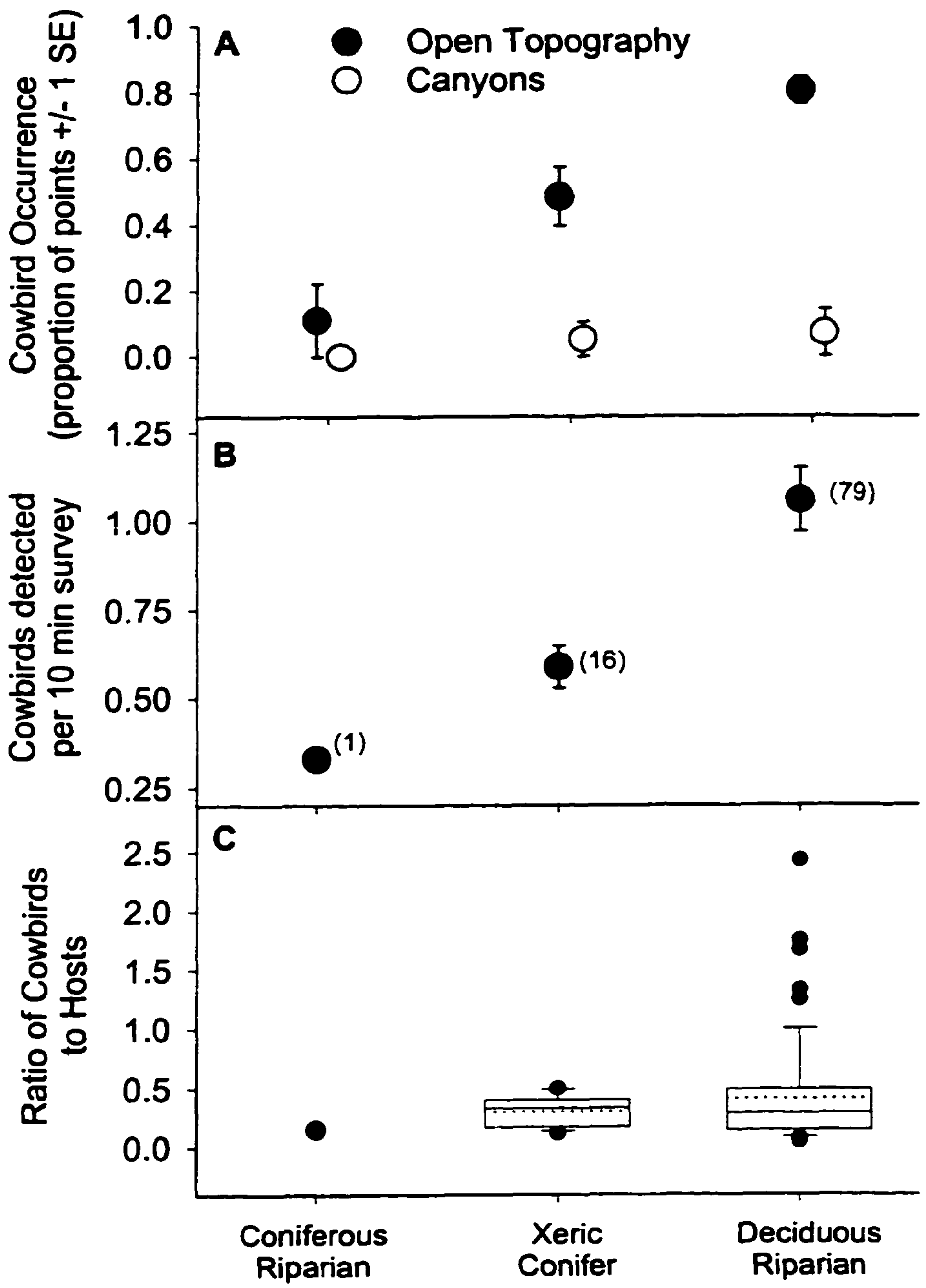
A
● Open Topography
○ Canyons
Cowbird Occurrence (proportion of points +/- 1 SE)
1.0
0.8
0.6
0.4
0.2
0.0
B
Cowbirds detected per 10 min survey
1.25
1.00
0.75
0.50
0.25
(1)
(16)
(79)
C
Ratio of Cowbirds to Hosts
2.5
2.0
1.5
1.0
0.5
0.0
Coniferous Riparian
Xeric Conifer
Deciduous Riparian

Figure 4

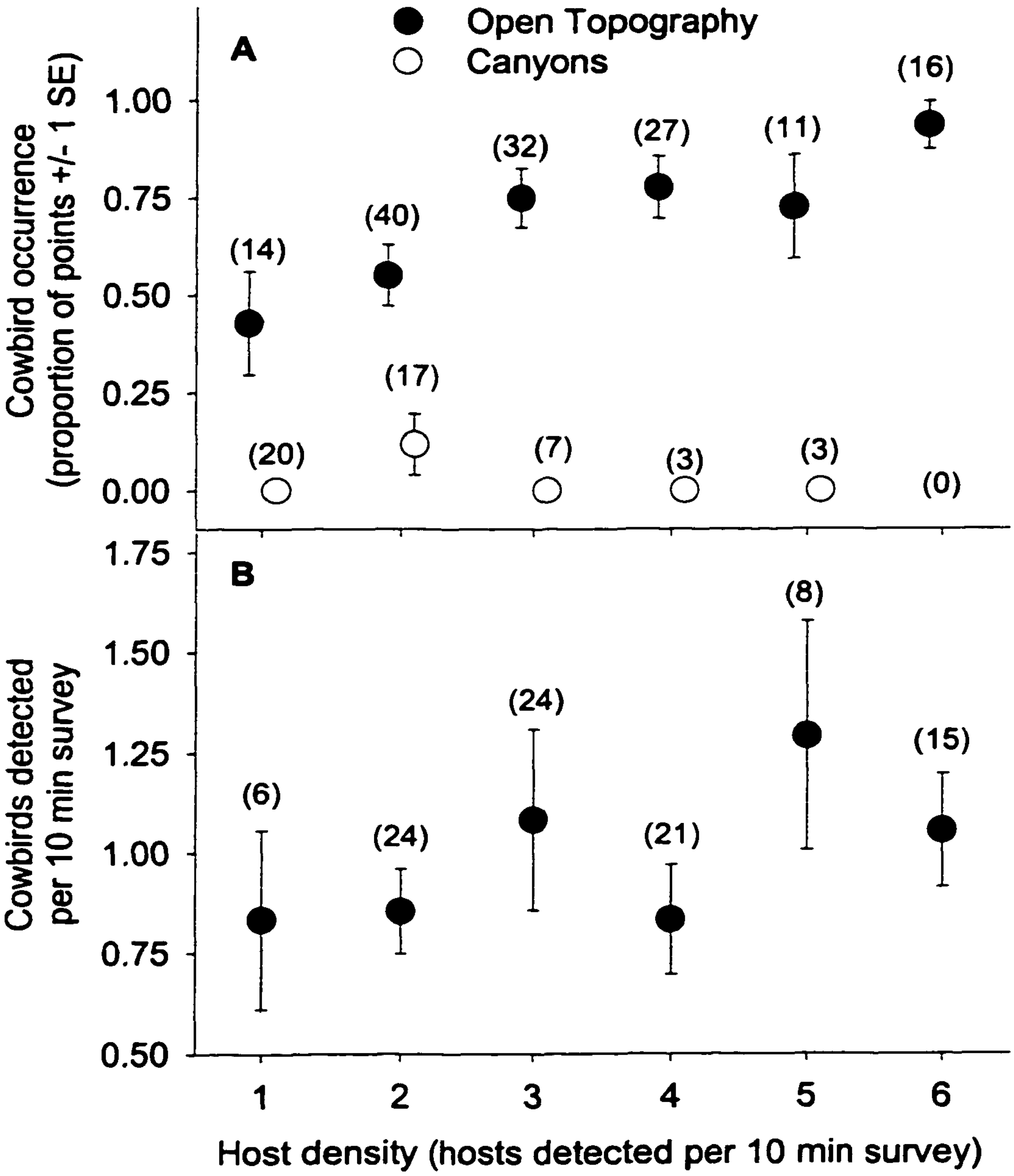
A
● Open Topography
○ Canyons
Cowbird occurrence (proportion of points +/- 1 SE)
1.00
0.75
0.50
0.25
0.00
(14)
(40)
(32)
(27)
(11)
(16)
(20)
(17)
(7)
(3)
(3)
(0)
B
Cowbirds detected per 10 min survey
1.75
1.50
1.25
1.00
0.75
0.50
(6)
(24)
(24)
(21)
(8)
(15)
1
2
3
4
5
6
Host density (hosts detected per 10 min survey)

Figure 5

Chapter 3

Can we really predict risk of cowbird parasitism with indirect measures?

Abstract

Management decisions involving parasitism often are based on parasitism risk inferred either from relative abundance of Brown-headed Cowbirds or from predictive relationships between landscape composition and brood parasitism. However, few studies have confirmed the accuracy of either of these indirect metrics in predicting parasitism rates. We conducted repeated surveys and monitored more than 2,600 nests on 16 deciduous riparian study plots in western Montana over three years. We compared the accuracy of four different cowbird survey metrics (all cowbirds detected, all cowbirds detected within 50 m, all female cowbirds detected, and all female cowbirds detected within 50 m) and the abundance of human habitations and agriculture at four landscape scales in predicting parasitism frequency (the percent of nests parasitized) and parasitism intensity (the number of cowbird eggs per parasitized nest). The number of female cowbirds detected provided the best fit with parasitism frequency, suggesting that sex determination during cowbird surveys will improve predictions of parasitism rates. Unlike parasitism frequency, parasitism intensity was not related to any measure of cowbird relative abundance. Similarly, parasitism frequency was strongly correlated with land-use patterns, but parasitism intensity was not. Parasitism frequency was best predicted at a 1 km radius landscape scale and was best predicted by the percentage of the landscape devoted to human habitation (e.g. farms and houses), rather than the percentage of the landscape devoted to agriculture. However, the relationship between human habitation and parasitism frequency was highly curvilinear; small changes in the density of human habitations may have large impacts on parasitism where these areas are scarce, but little impact where human habitation is abundant. Indirect measures may be useful in predicting parasitism frequency but the strength of these relationships depends on the metrics and scales used.

Key words: landscape fragmentation; landscape scale; brood parasitism; parasitism frequency; parasitism intensity; cowbird abundance; riparian birds; Brown-headed Cowbird; *Molothrus ater*; Yellow Warbler; *Dendroica petechia*; Warbling Vireo; *Vireo gilvus*; Song Sparrow; *Melospiza melodia*.

Introduction

High levels of brood parasitism by the Brown-headed Cowbird (*Molothrus ater*) can substantially reduce breeding productivity of host species and even threaten the persistence of host populations (Nolan 1978; Goldwasser et al. 1980; Marvil and Cruz 1989; Sealy 1992; Trail and Baptista 1993; McMaster and Sealy 1997). Low levels of brood parasitism, on the other hand, may pose little threat to the health of many species, especially those that often abandon parasitized nests or raise multiple broods in a season (Nolan 1978; Sedgwick and Knopf 1988; Hill and Sealy 1994; Smith and Arcese 1994; Sealy 1995). These conditional effects, combined with the large variance in parasitism among regions, habitats, and species, make the accurate assessment of the frequency (% of nests parasitized) and intensity of parasitism (number of cowbird eggs per parasitized nest) critically important. Direct assessment of parasitism frequency and intensity provides the most accurate information, but the intense effort needed to collect these data make direct determination impractical over broad geographic areas. Thus conservation decisions often rely on surveys to determine the relative abundance of cowbirds (Rich et al. 1994; Donovan et al. 1997; Hejl and Young 1999; Tewksbury et al. 1999; Young and Hutto 1999) or on models that use landscape variables to predict either cowbird abundance (Verner and Rothstein 1988; Rothstein 1994; Donovan et al. 1997; in press; Hejl and Young 1999; Tewksbury et al. 1999; Young and Hutto 1999) or rates of cowbird parasitism (Robinson 1992; Robinson et al. 1995; Tewksbury et al. 1998; Thompson et al. in press). The development of these less intensive methods to index parasitism is necessary, but the accuracy of these methods may depend on the metrics and scales used. Currently, untested assumptions surrounding both survey metrics and landscape models raise questions about the utility of these methods in predicting parasitism.

First, estimates of cowbird abundance are commonly assumed to index parasitism frequency and intensity, but this assumption is untested. Moreover, some studies report all cowbirds detected while others report only female cowbirds detected. The use of different metrics makes comparison across different studies difficult, and no studies have explicitly compared these metrics in a single study system. Second, different studies have examined different aspects of land use (e.g. agriculture, forest cover etc.) at varying landscape scales without examining the predictive ability of these land-uses across multiple scales (Hochachka et al. 1999). Studies from the Midwest have used large (10 km radius) landscape scales, and quantified landscape fragmentation as the percent of the landscape covered by forest (Donovan et al. 1995, 1997, in press; Robinson et al. 1995; Thompson et al. in press). However, forest cover is an indirect metric, because cowbird densities and parasitism rates are likely influenced by the type of habitat replacing cleared forests (Tewksbury et al. 1998). Indeed, studies in the West have used much smaller landscape scales and found strong relationships between parasitism rates and the percentage of the landscape devoted to human habitation (farms, corrals, and houses) and the proximity of agricultural areas (Tewksbury et al. 1998, 1999; Hejl and Young 1999; Young and Hutto1999), rather than the percentage of forested landscape. Ultimately, a rigorous examination of landscape scales and land-use features in a single system is needed.

We address these issues in deciduous riparian areas in the Bitterroot Valley of western Montana. Deciduous riparian areas are breeding grounds for the highest density and diversity of cowbird host species in the Western United States (Carothers 1974; Gaines 1977; Johnson et al. 1977; Dobkin 1994; Tewksbury et al. 1999). We explore the relationships between cowbird numbers, parasitism rates, and two land-uses (human habitation and agriculture) thought to directly influence cowbird numbers and parasitism rates. We first examine the relationships between parasitism frequency and intensity and the relative abundance of cowbirds to determine the cowbird abundance metric that best predicts parasitism. We then examine the abundance of these two land-uses at four different spatial scales to determine the landscape scale and the land-use characters that best predict parasitism pressure in the Bitterroot Valley.

Methods

Study area and study plots

The study was conducted in the Bitterroot Valley of western Montana. We established 16 plots in deciduous riparian areas set within local landscapes that ranged from highly fragmented by agriculture and human habitation to predominantly forested and unfragmented (Fig. 1). Much of the Bitterroot Valley is privately owned. We confined our overall study area to a 45 km section of the Bitterroot River, identified all relatively pristine deciduous riparian areas using aerial photographs, and contacted the owners of all the land we had identified. From the subset of areas where we received landowner permission, we chose study plots to maximize distance between plots and evenly sample the study area. All plots included here had either no record of recent grazing, or very light grazing pressure, predominantly in the late summer. The average size of our plots was 12 ha (range = 7 to 25 ha), and plots ranged from 1050 to 1350 m in elevation. Deciduous habitats in the Bitterroot Valley are often fairly continuous, thus plots did not include all habitat in a given location. All plots were dominated by deciduous trees and shrubs typical of either the black cottonwood (*Populus trichocarpa*) / red - osier dogwood (*Cornus stolonifera*) community type, the quaking aspen (*Populus tremuloides*) / red - osier dogwood vegetation type, or the mountain alder (*Alnus incana*) community type (Hansen et al. 1995).

Parasitism rates

During the breeding seasons of 1995 - 1997, we monitored more than 2,600 nests of 74 species to determine fledging success and parasitism rates using methods described in Martin and Geupel (1993). Brood parasitism was determined by checking nest status every two to four days using mirror poles and ladders to reach high nests. We found cowbird eggs in the nests of 24 species and determined parasitism status for a total 1055 host nests (Table 1). To examine community-wide parasitism frequency and intensity on each plot we identified primary hosts as the subset of species that accept cowbird eggs and that Brown-headed Cowbirds regularly parasitize (greater than 15% of nests parasitized, Table 1). We report community parasitism frequency and intensity from data pooled across primary hosts on each plot. We also present data for the three most common host species separately; Yellow Warblers *(Dendroica petechia)*, Warbling

Vireos (*Vireo gilvus*), and Song Sparrows (*Melospiza melodia*). Because parasitism frequency did not change significantly between years for any species considered (Yellow Warbler $\chi^2 = 0.458, p = 0.795$, Warbling Vireo $\chi^2 = 0.994, p = 0.608$, Song Sparrow $\chi^2 = 0.166, p = 0.92$, all other species p's > 0.35), we pooled data across the three years of study (Table 1).

We present data on parasitism intensity for the host community combined, and for Yellow Warblers, the only single host species for which we monitored a sufficient number of nests to examine parasitism intensity among plots. We were primarily interested in the realized impact of cowbirds on host species. Therefore, for analysis of parasitism intensity, we excluded nests abandoned or depredated before the completion of egg laying (62 cases, 33 Yellow Warbler). These nests were often not active long enough to be parasitized more than once and could thus bias estimates of the number of cowbird eggs per nest. We excluded one study plot from the analysis due to insufficient nests to determine parasitism intensity.

Cowbird abundance

We surveyed 82 points on our 16 study plots from 1995 through 1997. We established all points at least 200 m from all other points, at a density of one point per 2.5 ha, and surveyed each point three times per season. The number of point locations per plot ranged from 2 to 8. Each survey was 10 minutes long, and was conducted between ½ hour after sunrise and 11:00. During each survey, we recorded all cowbirds seen or heard in one of three distance classes; < 50 m, 50-100 m, and > 100 m from the observer. We surveyed 15 study plots in 1995, 16 in 1996, and 13 in 1997 and monitored nests on all plots surveyed.

To evaluate the effectiveness of different relative abundance metrics in indexing parasitism, we calculated the relative abundance of Brown-headed Cowbirds on our study plots in four different ways: (1) using all cowbird detections within 50 m of the survey point, (2) all detections at unlimited distance, (3) all female cowbird detections within 50 m, and (4) all female detections at unlimited distance. We averaged detections within each year for each survey point, then averaged across points and years to generate cowbird abundance metrics for each plot, which represent the total relative abundance of cowbirds on the plot over the course of the study. This was justified because parasitism rates did not differ across years and were also pooled (see earlier)

Landscapes

We mapped land-use and land-cover types around all study plots by examining 1:15,840 aerial photographs taken in 1994, delineating land type and land use polygons on orthophotoquads, and digitizing these into a Geographic Information System using PC ARC/INFO (ESRI 1989). We mapped all buildings and land uses, and verified land-cover type and land-use by field-checking the identity of all buildings and polygons during the study. Our minimum mapping unit was 0.065 ha.

Scale analysis

Human habitation appears to be a strong predictor of brood parasitism in the Bitterroot Valley (Tewksbury et al. 1998). Human habitation includes farm buildings, corrals, livestock holding areas, residential development and commercial development. The majority of human habitation in the Bitterroot Valley is rural development. Most houses have either a corral, bird feeder, or an area where chicken feed or grain is abundant, thus providing favorable foraging sites for cowbirds (Rothstein et al. 1980, 1987; Verner and Ritter 1983; Tewksbury et al. 1998). Here we examine the relationship between human habitation and parasitism rates at four landscape scales: all land within 0-0.5 km, 0-1 km, 0-2 km, and 0-3 km from each plot (Fig. 2). We also measured the percent agriculture around each plot at these four scales to compare the predictive power of these landscape variables. Two pairs of plots were too close to each other to consider landscapes to be independent (Fig. 1); in these cases we averaged parasitism frequency within each pair and combined landscape metrics for analysis.

Data analysis

We conducted linear regression for each cowbird abundance metric to determine which of the four metrics best predicted parasitism frequency and intensity. However, we first examined the potential for host density to modify the relationship between cowbird abundance and parasitism rates using partial regression analysis, because host density has been shown to affect parasitism rates in our system and elsewhere (Barber and Martin 1997; Tewksbury et al. 1998). Host density was calculated as the sum of all primary hosts detected within 50m of the observer. We did not consider unlimited distance counts for host density because differing detection probabilities of host species would be exaggerated as louder hosts are detected more often further from the observer (Hutto et al. 1986). Host density did not affect the relationship between cowbird abundance and parasitism rates (all *p*'s > 0.4), thus we present simple linear regression results. To examine the relationship between parasitism frequency and intensity, we used Pearson Correlation Analysis (SPSS 1996).

Before examining the predictive ability of human habitation and agriculture on parasitism, we log-transformed human habitation as it showed a strong nonlinear relationship with parasitism frequency. Both human habitation and agriculture varied considerably across scales, but because larger landscape scales included the smaller landscapes, measures of both variables were correlated among spatial scales (Pearson's correlation coefficient > 0.59 in all cases). At each scale, we examined simple correlations between each land-use and parasitism frequency and intensity. We also conducted partial correlations, controlling for the effect of one land-use while examining the effect of the other. By comparing correlation coefficients across scales, we assessed the change in the predictive strength of each land-use as we increased spatial scale.

Results

Cowbird abundance and parasitism

The relative abundance of female cowbirds was consistently a better predictor of parasitism frequency than the relative abundance of all cowbirds (Fig. 3). We found no consistent difference between the ability of 50 m fixed radius counts to predict parasitism frequency and the ability of unlimited distance counts (Fig. 3). However, unlimited distance counts of female cowbirds were the best overall predictor of community parasitism rates (Fig. 3A). Parasitism was positively related to the detection frequency of female cowbirds at unlimited distance for the three individual species, but these relationships were not as strong as the relationships for the community as a whole because of sample size limitations on individual species (Fig. 4). Parasitism intensity was weakly correlated with parasitism frequency at the community level (Fig. 5A), but strongly correlated within Yellow Warblers (Fig. 5B). Parasitism intensity was not related to any measure of cowbird abundance for the community as a whole ($r^2 = 0.059$, $p = 0.45$ for all cowbirds at 50 m; $r^2 = 0.09$, $p = 0.34$ for female cowbirds at all distance), or for Yellow Warblers ($r^2 = 0.34$, $p = 0.13$ for all cowbirds at 50 m; $r^2 = 0.38$, $p = 0.11$ for female cowbirds at all distance).

Parasitism and landscape variables

Agricultural land use and human habitation are confined to private land, and concentrated near the Bitterroot River (Fig. 1). Human land use varies along the valley, with more agriculture in the wider north end of the valley. While all of our study plots are within an area 44 km long and 6 km wide, landscape structure varies considerably around our plots (Figs.1 and 2).

Simple correlations between human habitation and parasitism frequency generally increased in strength from the 0.5 km scale to the 1 km scale, but generally did not increase at larger scales (Fig. 6A). In contrast, correlations with percent agriculture did not show a clear trend with changes in scale (Fig. 6B). Human habitation was positively correlated with agriculture in the Bitterroot Valley, regardless of scale ®= 0.60 to 0.67). However, partial correlations between parasitism frequency and human habitation remained highly significant after controlling for agriculture ®= 0.76, $p =$ 0.004 at the 0 - 1 km scale - Fig. 6C), while correlations between parasitism frequency and agriculture were not significant after controlling for human habitation ($p = 0.14$ to 0.47 - Fig. 6D). Additionally, partial correlations between human habitation and parasitism clearly peaked at the 1 km scale and declined at larger scales (Fig. 6C).

While the relationship between human habitation and parasitism frequency was strong, it was also highly nonlinear (Fig. 7). Where human habitation was scarce or non-existent, small increases in human habitation were associated with large increases in parasitism frequency, but where human habitation was common, plots with substantial differences in the human habitation had similar parasitism frequencies (Fig. 7).

Parasitism intensity was similar to parasitism frequency in that it was significantly correlated with human habitation, but not with agriculture. However, only three of the correlations were significant, two between the host community and human habitation ($r^2 = 0.772, p = 0.009$ at landscapes 0 to 2 km, and $r = 0.727, p = 0.017$ at 0 to

3 km landscapes) and one between Yellow Warblers and human habitation ®= 0.813, p = 0.014 at 0 to 1 km landscapes). No correlations between parasitism intensity and either land-use were significant in partial correlation, when the effect of one variable is controlled while the other is analyzed.

Discussion

Cowbird abundance and parasitism

Current assumptions regarding the ability of surveys to predict rates of brood parasitism have both some validity and some problems that need to be more fully recognized. Recent research has reported cowbird abundance as both male and female cowbirds pooled (Donovan et al. 1997; Hejl and Young 1999; Tewksbury et al. 1999; Young and Hutto 1999; Ward and Smith in press) or as female cowbirds alone (Donovan et al. in press; Thompson et al. in press). Our finding that female cowbird detections provide a more accurate assessment of parasitism frequency than male and female detections combined supports the practice of separating cowbird detections by sex based on song and call differences. Thus carefully designed studies reporting female cowbird abundance are likely accurately indexing relative parasitism frequency among locations (Figs. 3 and 4). However, direct nest monitoring will still be necessary for monitoring the health of individual species. The weak correlations we found between cowbird abundance and parasitism on individual species may reflect sample size limitations. However, strong correlations may not be expected, given that the host community does not remain constant from one plot to the next, and rates of parasitism on a particular species may be influenced by the abundance and quality of alternative hosts in an area (Martin and Barber 1997).

Cowbird abundance metrics did not predict community parasitism intensity because different host species varied considerably in parasitism intensity, even when they occur on the same plots and are similar in parasitism frequency. For example, Yellow Warblers and Song Sparrows did not differ in parasitism frequency (paired t-test among plots where they both occur: $df = 5$, $t = 0.187$, $p = 0.425$), but Song Sparrows averaged 2.17 eggs per nest, while Yellow Warblers averaged 1.28 eggs per nest (paired t-test: $df = 5$, $t = 2.48$ $p = 0.028$). These species specific differences in parasitism intensity could be due to active decisions by cowbirds based on host quality (Smith and Myers-Smith 1998) or to differences in nest location (Briskie et al. 1990). Regardless of the mechanism, coupled with natural variation in the composition of the host communities among plots, these differences explain the poor correlation between parasitism intensity and both cowbird abundance metrics and landscape variables. Our finding that parasitism intensity on the Yellow Warbler was only weakly related to cowbird abundance may indicate that parasitism intensity is also influenced by the abundance and quality of alternative hosts in an area (Smith and Myers-Smith 1998). Clearly, more work is needed to understand the relationship between the frequency and intensity of cowbird parasitism in the context of different host communities.

Land-use and parasitism

The majority of studies documenting landscape fragmentation effects on birds have defined fragmentation in terms of the percentage of forest cover on the landscape (Donovan et al. 1995, 1997, in press; Robinson et al. 1995; Thompson et al. in press). These studies often find strong relationships between parasitism and forest cover, but few studies have explicitly examined the effect of different types of land-use replacing the forest (Donovan et al. 1997; Tewksbury et al. 1998). In the Bitterroot Valley, human habitation never exceeds 12% of the landscape area, and agricultural land occupies 2 to 10 times as much land area as human habitation at all scales. However, human habitation was consistently a better predictor of parasitism frequency than agriculture (Fig. 6). Human habitation may be more closely tied to cowbird food resources, suggesting that the type of land-use replacing forest cover is important in determining parasitism.

While human habitation is the best predictor of parasitism frequency in the Bitterroot Valley, the nonlinear relationship between these variables makes accurate prediction of parasitism difficult. Small changes in the density or location of houses, farms and corrals appear to have large impacts on parasitism frequency where these feeding resources are rare on the landscape, but similar changes have little effect where feeding resources are abundant (Fig. 7). This nonlinear relationship likely reflects a shift in the resources limiting cowbird numbers on our plots. Where feeding locations are scarce or distant, as in the forested habitats in the Bitterroot Valley, small changes in the abundance of feeding resources may attract more cowbirds into an area. As a single female cowbird can lay as many as 40 eggs in a season (Scott and Ankney 1983; Fleischer et al. 1987), the addition of a few females may make a large difference in parasitism frequency. In contrast, where feeding resources are abundant, changes in the abundance, distribution, or quality of these resources may have little impact. In these landscapes, cowbird numbers may be limited by the breeding resources on the landscape (forested habitats) and territorial interactions among cowbirds. This latter situation may characterize much of the Midwest, where forested islands are often surrounded by large expanses of agriculture and human habitation, and it could explain the strong correlations found between parasitism rates and forest cover in those landscapes.

Landscape scale and parasitism

Most studies to date have examined landscape impacts on parasitism frequency at broad spatial scales, and parasitism rates are often pooled across study plots within each large landscape (Donovan et al. 1995; Robinson et al. 1995; Hochachka et al. 1999; Thompson et al. 1999). While this may be appropriate in the relatively simple landscapes of the Midwest, we found that local scales provided the highest correlations between parasitism frequency and human habitation. When we considered landscapes > 2 km from our study plots, our ability to predict parasitism frequency decreased. Moreover, all of our study plots were within a 264 km^2 area, yet parasitism frequency varied from 12 - 76% among plots, and similar plots as close as 4 km to each other differed in parasitism frequency by as much as 40%. These results suggest strong local scale or neighborhood effects (Dunning et al.1992). The 10 km radius landscapes often used in Midwestern studies include 314 km^2 around each study plot — an area larger than our entire study system. While such broad landscape scales may be useful when comparing across regions, they clearly can obscure the large differences in parasitism frequency found at local scales. In the West, landscape analysis at local scales may provide more accurate predictions of parasitism frequency and more concrete land-management directives than the use of larger landscape scales.

The greater predictive properties of the 1 km landscape scale (Fig. 6) may be a reflection of the distance traveled by cowbirds. We radio-tracked nine female cowbirds in 1996, and found that all nine birds had defined breeding territories. The average travel distance between feeding and laying areas was < 1 km, but females often traveled > 500 m between these areas (Tewksbury and Johnson, unpubl. data). In a much larger study of cowbird movements, Thompson (1994) found a similar pattern with mean movement distances less than 1 km between foraging and laying areas. However, in more forested areas where breeding and feeding resources are farther separated, movement distances between breeding and feeding areas are longer (Gates and Evans 1998). In these areas, larger landscapes may be more useful in determining parasitism frequency.

Conclusions

The accurate prediction of parasitism frequency and intensity using indirect measures will require careful selection of metrics, and the recognition that landscape features used to predict parasitism at regional scales may obscure important differences in parasitism at local scales. Similar shifts in the predictive variables may also occur as the degree of human alteration and fragmentation of the landscape changes and cowbird numbers become limited by different resources. Ultimately the management of landscapes to reduce the impact of cowbirds may be best served by a multi-scale approach that concentrates on local neighborhood effects without ignoring regional land-use impacts. This approach may allow us to preserve high-quality breeding areas even in extensively fragmented landscapes by manipulating local-scale features immediately adjacent to conservation areas.

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Literature Cited

Barber, D. R. and T. E. Martin. 1997. Influence of alternate host densities on Brown-headed Cowbird parasitism rates in Black-capped Vireos. Condor **99**:595-604.

Briskie, J. V., S. G. Sealy, and K. A. Hobson. 1990. Differential parasitism of Least Flycatchers and Yellow Warblers by the Brown-headed Cowbird. Behavioral Ecology and Sociobiology **27**:403-410.

Carothers, S. W. 1974. Population structure and social organization of Southwestern riparian birds. American Zoology **14**:97-108.

Dobkin, D. S. 1994. Conservation and management of neotropical migrant landbirds in the northern Rockies and great plains, University of Idaho Press, Moscow, Idaho.

Donovan, T. M., P. W. Jones, E. M. Annand, and F. R. I. Thompson. 1997. Variation in local-scale edge effects: mechanisms and landscape context. Ecology **78**:2064-2075.

Donovan, T. M., F. R. Thompson III, J. Faaborg, and J. R. Probst. 1995. Reproductive success of migratory birds in habitat sources and sinks. Conservation Biology **9**:1380-1395.

Donovan, T. M., F. R. Thompson III, and J. Faaborg. in press. Cowbird distribution at different scales of fragmentation: tradeoffs between breeding and feeding opportunities. in T. Cook, S. K. Robinson, S. I. Rothstein, S. G. Sealy, and J. N. M. Smith, editors. Ecology and Management of Cowbirds. University of Texas Press, Austin, TX.

Dunning, J. B., B. J. Danielson, and H. R. Pulliam. 1992. Ecological processes that affect populations in complex landscapes. Oikos **65:**169-175.

ESRI. 1989. PC Arc Info, Environmental Systems Research Institute, Inc., Redlands, CA.

Fleischer, R. C., A. P. Smyth, and S. I. Rothstein. 1987. Temporal and age-related variation in the laying rate of the parasitic Brown-headed Cowbird in the eastern Sierra Nevada, California (USA). Canadian Journal of Zoology **65:**2724-2730.

Gaines, D. 1977. The valley riparian forests of California: their ecology and conservation, Institute of Ecology; University of California, Davis, CA.

Gates, J. E. and D. R. Evans. 1998. Cowbirds breeding in the Central Appalachians: spatial and temporal patterns and habitat selection. Ecological Applications **8:**27-40.

Goldwasser, S., D. Gaines, and S. R. Wilbur. 1980. The Least Bell's Vireo in California: a de facto endangered race. American Birds **34:**742-745.

Hansen, P. L., R. D. Pfister, K. Boggs, B. J. Cook, J. Joy, and D. K. Hinckley. 1995. Classification and management of Montana's riparian and wetland sites, vol. **54,** Montana Forest and Conservation Experiment Station, Missoula, MT.

Hejl, S. J. and J. S. Young. 1999. Brown-headed Cowbirds in ponderosa pine/Douglas-fir-dominated landscapes in the northern Rocky Mountains. Studies in Avian Biology **18:**73-79

Hill, D. P. and S. G. Sealy. 1994. Desertion of nests parasitized by cowbirds: Have Clay-colored Sparrows evolved an anti-parasite defense? Animal Behavior **48:**1063-1070.

Hochachka, W. M., T. E. Martin, J. A. Collazo, E. E. Klass, D. Curson, P. B. Wood, T. Donovan, D. M. Evans, M. Knutson, J. Manolis, G. Geupel, K. P. McFarland, V. Artman, L. Garner, N. Mathews, J. Tewksbury, C. Geugen, L. Petit, S. Garner, D. Anderson, K. L. Purcell, J. Faaborg, R. Dettmers, C. R. Smith, D. Whitehead, and S. J. Hejl. 1999. Scale dependence in the effects of forest coverage on parasitism by Brown-headed Cowbirds. Studies in Avian Biology 18:??-??

Hutto, R. L., S. M. Pletschet, and P. Hendricks. 1986. A fixed radius point count method for nonbreeding and breeding season use. Auk **103:**593-602.

Johnson, R. R., L. T. Haight, and J. M. Simpson. 1977. Endangered species vs. endangered habitats: a concept. Pages 86-79 in R. R. Johnson and D. A. Jones, editors. Importance, preservation, and management of riparian habitat: a symposium. USDA Forest Service General Technical Report RM-43. Rocky Mountain Forest and Range Experiment Station, Fort Collins, CO.

Martin, T. E. and G. R. Geupel. 1993. Nest-monitoring plots: methods for locating nests and monitoring success. Journal of Field Ornithology **64:**507-519.

Marvil, R. E. and A. Cruz. 1989. Impact of Brown-headed Cowbird parasitism on the reproductive success of the Solitary Vireo. Auk **106:**476-480.

McMaster, D. G. and S. G. Sealy. 1997. Host-egg removal by Brown-headed Cowbirds: a test of the host incubation limit hypothesis. Auk **114:**212-220.

Nolan, V. Jr. 1978. The ecology and behavior of the Prairie Warbler *Dendroica discolor*, vol. **26**, American Ornithologists Union, Washington, DC.

Rich, A. C., D. S. Dobkin, and L. J. Niles. 1994. Defining forest fragmentation by corridor width: The influence of narrow forest-dividing corridors on forest-nesting birds in southern New Jersey. Conservation Biology **8:**1109-1121.

Robinson, S. K. 1992. Population dynamics of breeding Neotropical migrants in a fragmented Illinois landscape. Pages 408-418 in J. M. Hagan and D. W. Johnson, editors. Smithsonian Institute Press, Washington D.C.

Robinson, S. K., F. R. I. Thompson, T. M. Donovan, D. R. Whitehead, and J. Faaborg. 1995. Regional forest fragmentation and the nesting success of migratory birds. Science **267:**1987-1990.

Rothstein, S. I. 1994. The cowbird's invasion of the Far West: history, causes and consequences experienced by host species. Studies in Avian Biology **15:**301-315.

Rothstein, S. I., J. Verner, and E. Stevens. 1980. Range expansion and diurnal changes in dispersion of the Brown-headed Cowbird (*Molothrus ater*) in the Sierra Nevada, California, USA. Auk **97:**253-267.

Rothstein, S. I., J. Verner, E. Stevens, and L. V. Ritter. 1987. Behavioral differences among sex and age classes of the Brown-headed Cowbird and their relation to the efficacy of a control program. Wilson Bulletin **99:**322-337.

Scott, D. M. and C. D. Ankney. 1983. The laying cycle of Brown-headed Cowbirds (*Molothrus ater*): passerine chickens? Auk **100:**583-592.

Sealy, S. G. 1995. Burial of cowbird eggs by parasitized Yellow Warblers: an empirical and experimental study. Animal Behavior **49:**877-889.

Sealy, S. G. 1992. Removal of Yellow Warbler eggs in association with cowbird parasitism. Condor **94:**40-54.

Sedgwick, J. A. and F. L. Knopf. 1988. A high incidence of Brown-headed Cowbird parasitism of Willow Flycatchers. Condor **90:** 253-256.

Smith, J. N. M. and P. Arcese. 1994. Brown-headed Cowbirds and an island population of Song Sparrows: a 16-year study. Condor **96:**916-934.

Smith, J. N. M. and I. H. Myers-Smith. 1998. Spatial variation in parasitism of Song Sparrows by Brown-headed Cowbirds. Pages 295-312 in S. I. Rothstein and S. K. Robinson, editors. Parasitic birds and their hosts. Oxford University Press, New York.

SPSS. 1996. Advanced statistics 7.0 , SPSS, Incorporated, Chicago, Illinois, USA.

Tewksbury, J. J., S. J. Hejl, and T. E. Martin. 1998. Habitat fragmentation in a Western landscape: breeding productivity does not decline with increasing fragmentation. Ecology **79:**2890-2903.

Tewksbury, J. J., T. E. Martin, S. J. Hejl, T. S. Redman, and F. J. Wheeler. 1999. Cowbirds in a western valley: effects of landscape structure, vegetation and host density. Studies in Avian Biology **18**:23-33.

Thompson, F. R. I. 1994. Temporal and spatial patterns of breeding Brown-headed Cowbirds in the Midwestern United States. Auk **111:**979-990.

Thompson, F. R. I., S. K. Robinson, T. M. Donovan, J. Faaborg, and D. Whitehead. in press. Biogeographic, landscape, and local factors affecting parasitism levels. in T. Cooke, S. K. Robinson, S. I. Rothstein, S. G. Sealy, and J. N. M. Smith, editors. Ecology and management of cowbirds. University of Texas Press, Austin, Texas, USA.

Trail, P. W. and L. F. Baptista. 1993. The impact of Brown-headed Cowbird parasitism on populations of the Nuttall's White-Crowned Sparrow. Conservation Biology **7**:309-315.

Verner, J. and L. V. Ritter. 1983. Current status of the Brown-headed Cowbird (*Molothrus ater*) in the Sierra National Forest (USA). Auk **100**:355-368.

Verner, J. and S. I. Rothstein. 1988. Implications of range expansion into the Sierra Nevada by the parasitic Brown-headed Cowbird. Pages 92-98 in D. Bradley, editor. State of the Sierra Symposium Pacific Publishing Co, San Francisco, CA.

Ward, D. and J. N. M. Smith. in press. Inter-habitat differences in parasitism frequencies by Brown-headed Cowbirds in the Okanagan Valley, British Columbia. in T. Cook, S. K. Robinson, S. I. Rothstein, S. G. Sealy, and J. N. M. Smith, editors. University of Texas Press, Austin, TX.

Young, J. S. and R. L. Hutto. 1999. Habitat and landscape factors affecting cowbird distribution in the Northern Rockies. Studies in Avian Biology **18**:41-51.

Table 1: Parasitism frequency (percent of nests parasitized) and intensity (cowbird eggs per parasitized nest) for species parasitized by the Brown-headed Cowbird. Data for all three years of the study. Primary hosts (*) are species with greater than 15% of their nests parasitized.

Species	parasitism frequency (nests[†])	parasitism intensity (nests[¶])
Warbling Vireo (*Vireo gilvus*)*	58 (108)	1.42 (38)
Song Sparrow (*Melospiza melodia*)*	54 (74)	2.17 (30)
Yellow Warbler (*Dendroica petechia*)*	54 (257)	1.28 (71)
Veery (*Catharus fuscescens*)*	44 (16)	1.20 (5)
Solitary Vireo (*Vireo solitarius*)*	43 (21)	1.38 (8)
Willow Flycatcher (*Empidonax trailii*)*	41 (59)	1.00 (13)
American Redstart (*Dendroica ruticilla*)*	37 (97)	1.17 (17)
MacGillivray's Warbler (*Oporornis tolmiei*)*	32 (25)	1.00 (5)
Dusky Flycatcher (*Empidonax wrightii*)*	26 (106)	1.14 (22)
Black-headed Grosbeak (*Pheucticus melanocephalus*)*	18 (39)	1.33 (6)
Chipping Sparrow (*Spizela passerina*)	10 (20)	---
Western Wood-pewee (*Contopus sordidulus*)	10 (40)	---
Swainson's Thrush (*Catharus Ustuatus*)	9 (32)	1.00 (3)
Dark-eyed Junco (*Junco hyemalis*)	8 (24)	---

Table 1 (cont.)

Cedar Waxwing (*Bombycilla cedrorum*)	8 (40)	1.67 (3)
Red-winged Blackbird (*Agelaius phoeniceus*)	5 (43)	---

Less abundant host species

Species	parasitism frequency (nests[†])	parasitism intensity (nests[¶])
Audubon's Warbler (*Dendroica coronata*)*	100 (6)	1.00 (3)
Lazuli Bunting (*Passerina amoena*)*	100 (4)	1.00 (3)
Red-eyed Vireo (*Vireo olivaceus*)*	88 (8)	1.5 (6)
Common Yellowthroat (*Geothlypis trichas*)*	60 (10)	3.00 (3)
Nashville Warbler (*Vermivora ruficapilla*)*	50 (2)	2.00 (1)
Orange-crowned Warbler (*Vermivora celata*)*	43 (7)	2.00 (3)
Hammond's Flycatcher (*Empidonax hammondii*)*	33 (6)	1.00 (2)
Gray Catbird (*Dumetella carolinensis*)	9 (11)	—

† = numbers of nests monitored with known parasitism (from 1995 and 1997).

¶ = number of parasitized nests that survived past egg laying and the exact number of cowbird eggs was determined.

Figure Legends

Fig. 1. Study plot locations (points) and general agricultural land use in the Bitterroot Valley. Pairs of plots in circles are analyzed as one plot for landscape analysis due to non-independent landscapes (see methods).

Fig. 2. Detail of 3 study plots showing agriculture and human habitation cover at the 4 spatial scales analyzed (0 to 0.5 km, 0 to 1 km, 0 to 2 km and 0 to 3 km).

Fig. 3. Comparison of correlation coefficients (r values) among the four different parasitism metrics, when regressed against parasitism frequency. Regressions for female cowbirds at all distances are shown in Figure 5. Significance of regressions are denoted by stars (* = $P < 0.05$, ** = $P < 0.005$).

Fig. 4. Relationship between female cowbird detections at unlimited distance and parasitism frequency for the entire host community (A) and each of the three individual species tested.

Fig. 5. Relationship between parasitism frequency and parasitism intensity, for the community of primary hosts (A) and for Yellow Warblers (B). R's and P's are Pearson's correlation coefficients and related significance. Transformation of Yellow Warbler data did not improve the relationship.

Fig. 6: Simple correlation coefficients (A and B) and partial correlation coefficients (C and D) between parasitism frequency and percent human habitation (left) and percent agriculture (right) plotted at the four landscape scales analyzed. Correlations are presented for community parasitism (solid black line), Yellow Warblers (triangles), Warbling Vireos (circles), and Song Sparrows (squares). *'s indicate the significance of each correlation (* = $P < 0.05$, ** = $P < 0.005$).

Fig. 7: Relationship between community level parasitism pressure and percent human habitation at the 1 km landscape scale. We used transformed data for the correlations in figure 6 (B and D).

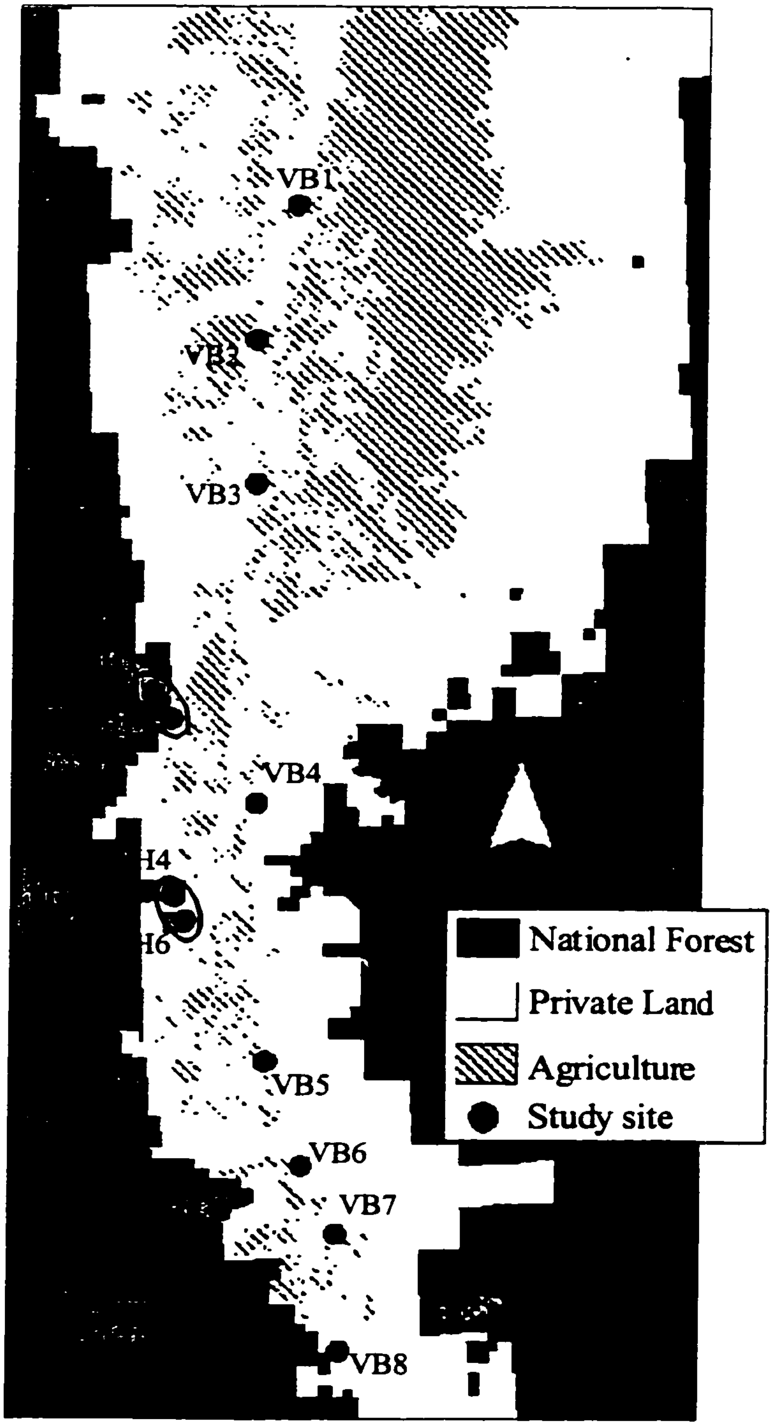
VB1
VB2
VB3
VB4
H4
H6
VB5
VB6
VB7
VB8
National Forest
Private Land
Agriculture
Study site

Figure 1

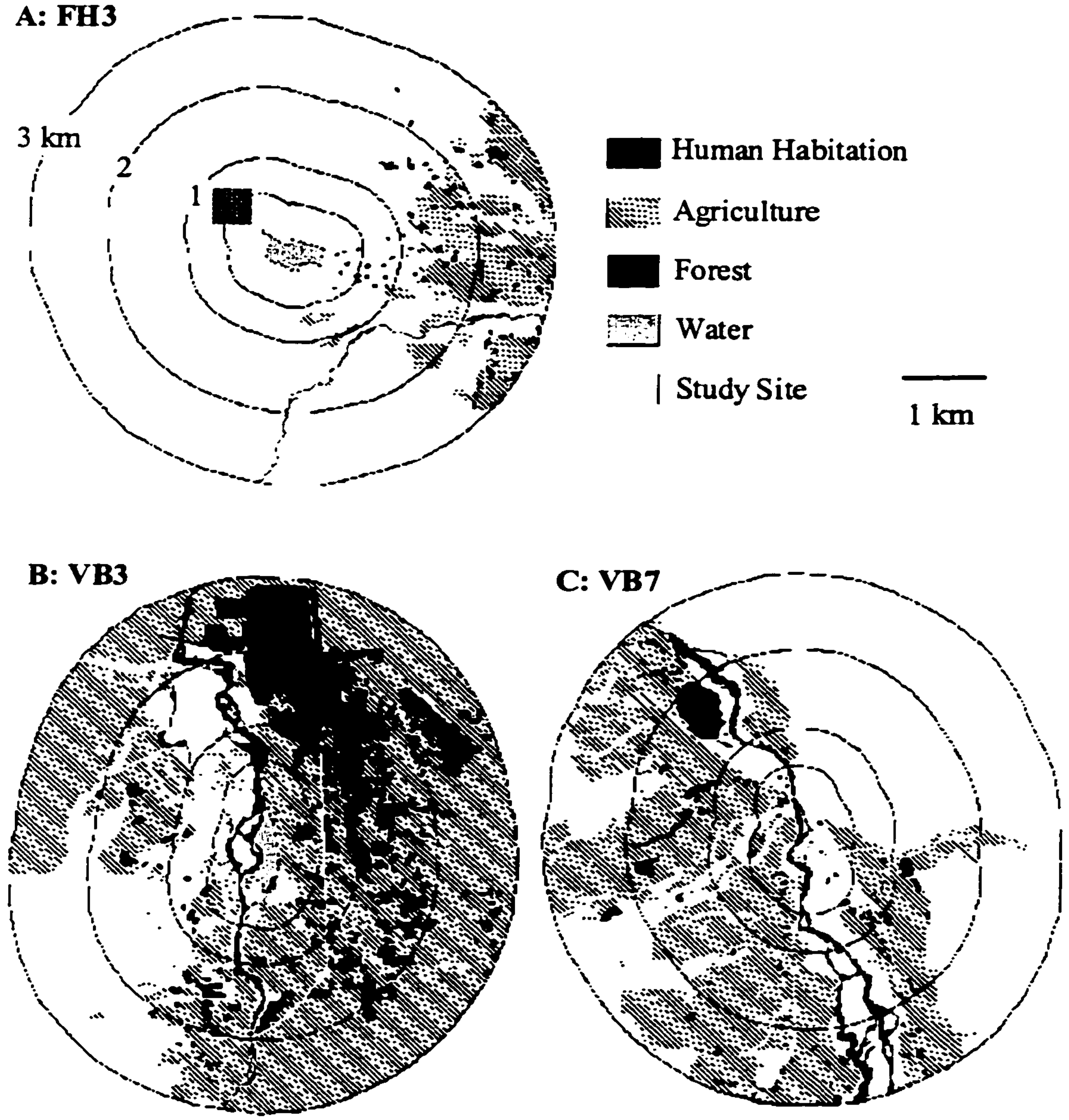
A: FH3
3 km
2
1
Human Habitation
Agriculture
Forest
Water
Study Site
1 km
B: VB3
C: VB7

Figure 2

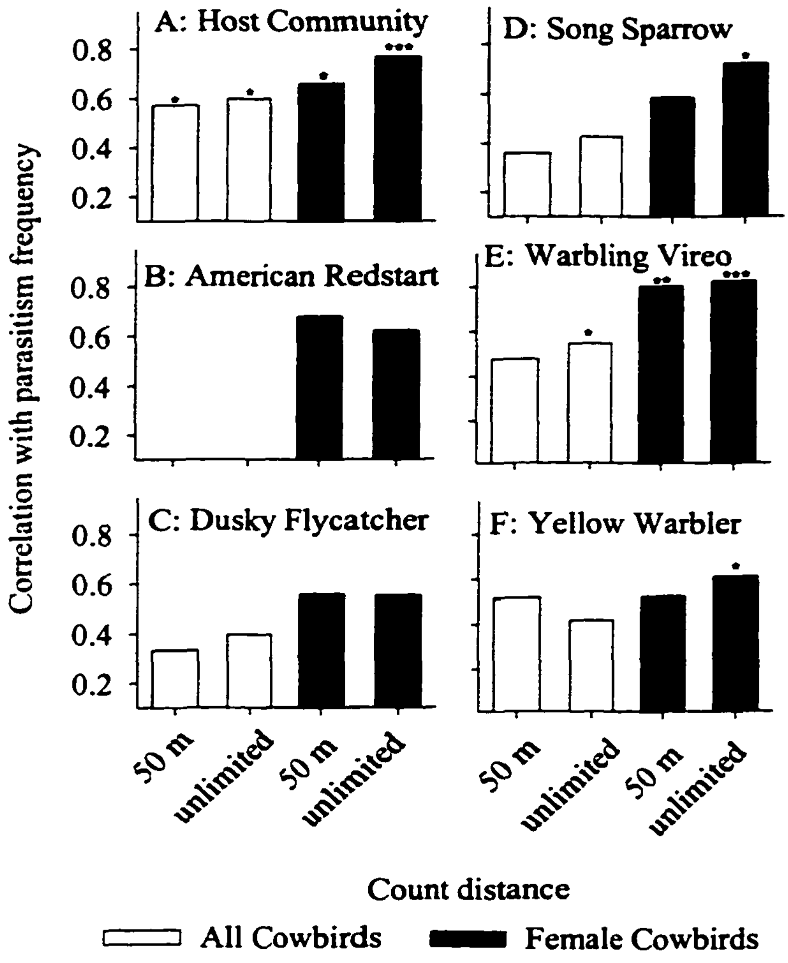
Correlation with parasitism frequency
0.8
0.6
0.4
0.2
A: Host Community
*
*
*
***
B: American Redstart
C: Dusky Flycatcher
D: Song Sparrow
*
E: Warbling Vireo
*
**
***
F: Yellow Warbler
*
50 m
unlimited
50 m
unlimited
50 m
unlimited
50 m
unlimited
Count distance
All Cowbirds
Female Cowbirds

Figure 3

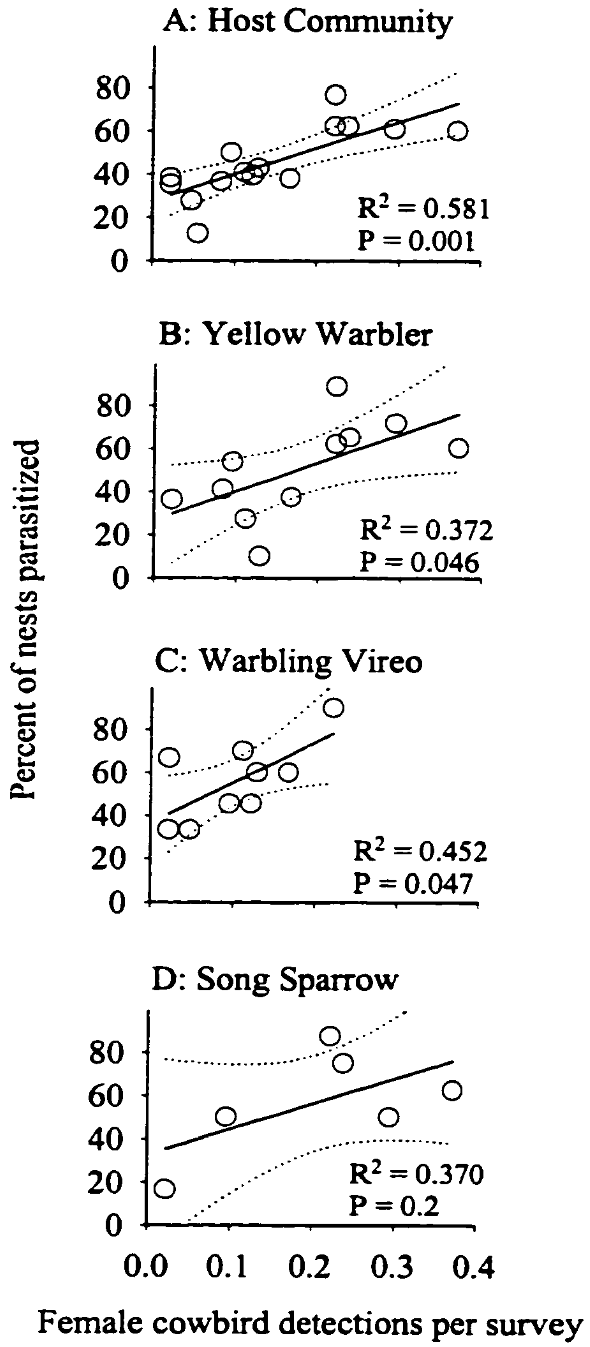
A: Host Community
R² = 0.581
P = 0.001
B: Yellow Warbler
R² = 0.372
P = 0.046
C: Warbling Vireo
R² = 0.452
P = 0.047
D: Song Sparrow
R² = 0.370
P = 0.2
0
20
40
60
80
0.0
0.1
0.2
0.3
0.4
Percent of nests parasitized
Female cowbird detections per survey

Figure 4

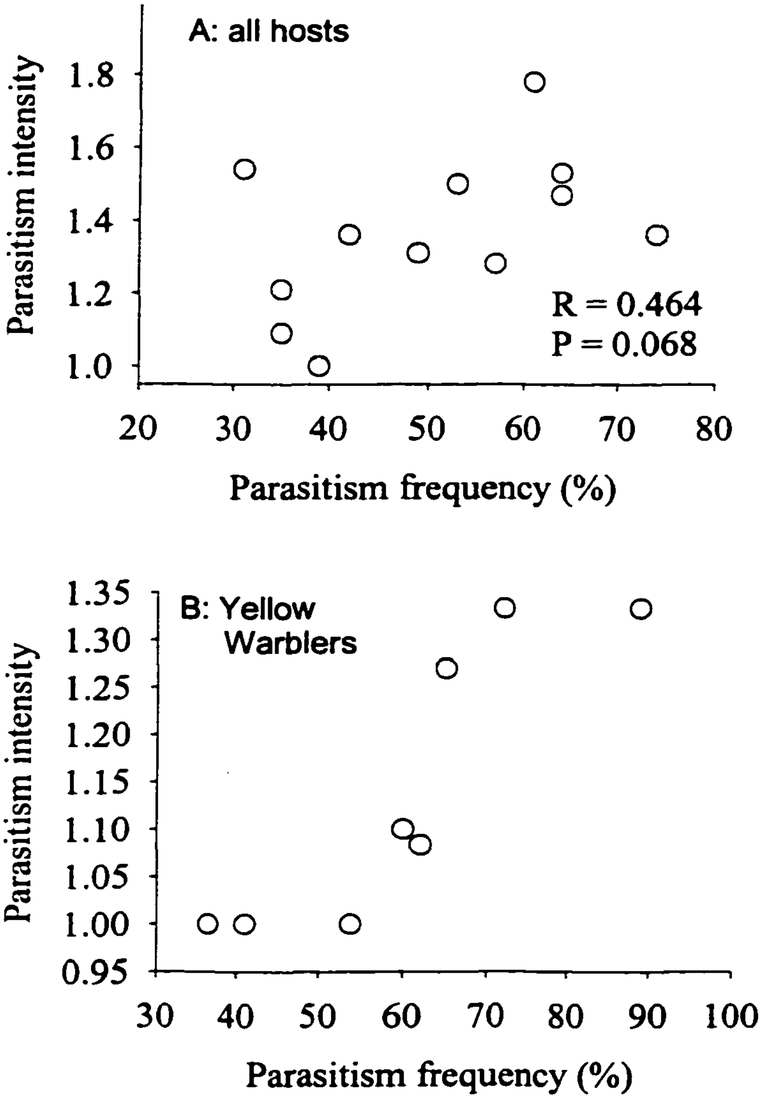
A: all hosts
Parasitism intensity
1.8
1.6
1.4
1.2
1.0
R = 0.464
P = 0.068
20
30
40
50
60
70
80
Parasitism frequency (%)
B: Yellow Warblers
Parasitism intensity
1.35
1.30
1.25
1.20
1.15
1.10
1.05
1.00
0.95
30
40
50
60
70
80
90
100
Parasitism frequency (%)

Figure 5

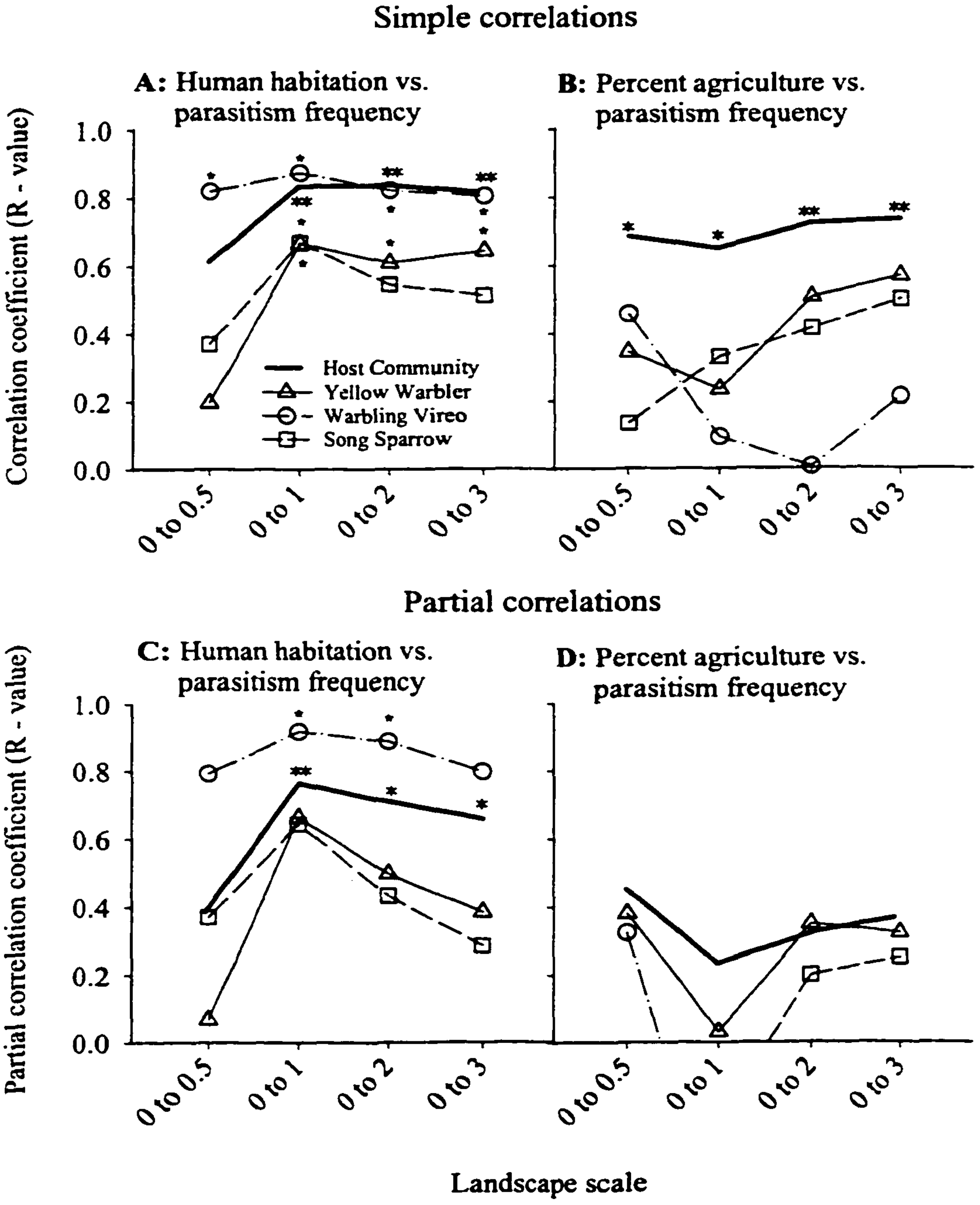
Simple correlations
A: Human habitation vs. parasitism frequency
B: Percent agriculture vs. parasitism frequency
Correlation coefficient (R - value)
1.0
0.8
0.6
0.4
0.2
0.0
Host Community
Yellow Warbler
Warbling Vireo
Song Sparrow
*
**
0 to 0.5
0 to 1
0 to 2
0 to 3
Partial correlations
C: Human habitation vs. parasitism frequency
D: Percent agriculture vs. parasitism frequency
Partial correlation coefficient (R - value)
Landscape scale

Figure 6

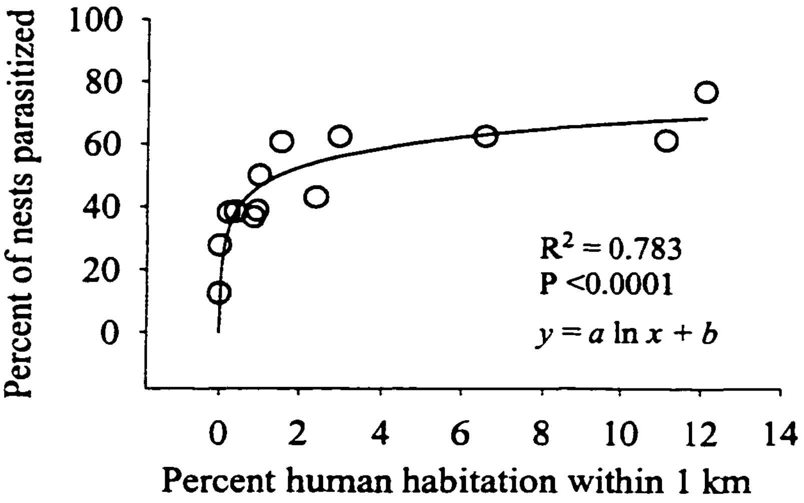
Percent of nests parasitized
100
80
60
40
20
0
0
2
4
6
8
10
12
14
Percent human habitation within 1 km
$R^2 = 0.783$
P <0.0001
$y = a \ln x + b$

Figure 7

Chapter 4

Parental Behavior of a Cowbird Host:

Caught Between Egg-Removal and Nest Predation

Abstract

Brood parasites remove eggs of their hosts, but the fitness consequences and responses of parents to egg-removal have been overlooked. We demonstrate that egg-removal causes clear fitness costs for the host. Experiments and observations provide the first documentation that female parents respond to the threat of egg-removal by spending more time on the nest, and that this behavior reduces risk of egg removal. Increased time on the nest, however, requires males to visit the nest more often to feed females and this increased activity increases nest predation. Thus birds are caught between the cost of egg-removal by brood parasites and the cost of increased nest predation when they attempt to reduce egg-removal.

Text

Brood parasitism, where a parasite lays an egg in the nest of a host, is a common threat to birds; over 240 bird species are parasitized by the Brown-headed Cowbird (*Molothrus ater*) in North America alone (*2*). Addition of cowbird eggs creates eventual fitness costs for hosts because competition for food among young can cause starvation or reduced growth of host young (*1-3*). Many host species reduce these egg addition costs by rejecting eggs. However, cowbirds typically make at least 2 trips to a nest, one to lay their own egg, and a second to remove a natal egg (*3*). Hosts incur an immediate fitness cost when cowbirds remove their eggs. For example, removal of one egg from a successful nest in a single-brooded host species can reduce annual reproductive success by 25% or more (*4*). Such reductions in reproductive success should strongly favor behaviors that minimize probability of egg removal. Here, we provide the first documentation of parental behavior that reduces egg removal by cowbirds; females can protect their eggs from cowbirds by spending more time on the nest (attentiveness). However, increased attentiveness is dependent on increased rates of incubation feeding, where males feed females on the nest (*5,6*). The resulting increase in visitation rate of males to the nest may increase nest predation rates (*7*), which can favor reduced incubation feeding rates (*6*). Nest predation costs, thus, oppose parasitism costs in their selection on parental behavior. Here, we experimentally test the behavioral responses and fitness consequences to these counterposing selection pressures for Yellow Warblers (*Dendroica petechia*) in Western Montana (*8*).

Birds are frequently parasitized by cowbirds in the Bitterroot Valley, Montana (*9*) and egg-removal is common (Fig. 1A); all species parasitized by cowbirds on our study sites had smaller clutches in parasitized nests suggesting that cowbirds remove natal-eggs from virtually all species they parasitize on our sites. These patterns are typified by Yellow Warblers, where parasitism is frequent (*10*) and parasitized nests lose an average of 1.32 natal eggs from cowbirds (Fig. 1A) during the egg-laying and incubation phase (*11*).

Egg-removal provides benefits to cowbird nestlings because the number of feeding visits directed to cowbird young increases as the number of natal young in the nest decreases (Fig. 1B). In contrast, egg-removal clearly decreased fitness (number of young fledged) in parasitized Yellow Warblers (Fig. 1C). Natal egg-removal was almost always prevented when the female Yellow Warbler was present on the nest (Fig. 2A), but female presence did not prevent cowbirds from laying eggs (Fig. 2A) (*13,14*). The different success of cowbirds at laying versus removing eggs in the presence of the host female might be explained as follows. Cowbirds require a nest in which to lay their eggs. If a cowbird has located only a single nest, then selection is strong to gain access to the nest and we have recorded multiple occurrences of cowbirds physically evicting the female host if she is found on the nest (*16*). Such aggressive behavior explains the success of cowbirds in laying eggs (Fig 2A). In contrast, even though natal egg-removal benefits the cowbird nestling (Fig. 1B), disturbance to the female host may increase the risk of nest abandonment or damage to the cowbird's egg (*17*). Thus, selection for cowbirds to forcibly evict the host female to remove a host egg may be much weaker than to lay an egg. Indeed, we found that cowbirds physically dragged the host female from the nest in every egg-laying event in which the female was encountered on the nest (n = 5). In direct contrast, frequency of physical interaction when cowbirds encountered the host female on the nest during an egg-removal attempt (4 of 24 cases) was dramatically lower ($G = 172$, $P < 0.0005$).

Given the ability of host females to reduce egg-removal by staying on the nest, this behavior should be favored where the risk of egg-removal is high. Parasitized nests run a significant risk of egg-removal even before the cowbird lays in the nest, but the chance of that host losing a natal egg jumps to 69% over the next 48 hours (Fig. 2B). Thus, increased egg-protection should be favored even for currently unparasitized individuals in areas of high parasitism risk, but selection for increased attentiveness should be even stronger after a cowbird lays an egg in a host's nest. We found support for both predictions.

Female Yellow Warblers increased their attentiveness with increased general risk of parasitism (Fig. 3A). Attentiveness is relatively low in unparasitized nests in areas where the risk of parasitism is low, but increases significantly in parasitized nests in these areas (Fig 3B). In contrast, on sites where the risk of parasitism is high, even unparasitized nests have high attentiveness and, thus, attentiveness does not differ from naturally parasitized nests (Fig 3B). These shifts in attentiveness cannot be explained by differences in nest temperature ($r = -0.093$, $P = 0.826$) or predation rates ($r = 0.35$, $P = 0.36$) among nests (*18*).

We experimentally tested these patterns by artificially parasitizing nests by presenting cowbird vocalizations at the nest and then placing a warmed cowbird egg in the nest (*19*). These tests were performed in the areas where the risk of parasitism is high; thus the results are highly conservative because attentiveness is already elevated in these areas (Fig. 3B) and expected shifts are small. Nevertheless, attentiveness significantly increased at unparasitized nests that were experimentally parasitized regardless of initial attentiveness (Fig. 3C). And, these results cannot be explained by clutch volume (*20*). Moreover, both unparasitized control nests, where a control model was presented and a host egg was replaced, and naturally parasitized nests showed no change in attentiveness over the same period (Fig. 3C; *P*'s > 0.6). The latter results mirror the absence of differences in attentiveness between unparasitized and parasitized nests in these high risk areas (see Fig. 2B). The benefits of these increases in attentiveness are clear; naturally parasitized nests in which cowbirds removed natal eggs had significantly lower attentiveness than those that did not lose natal eggs (Fig 3D).

The rate that males fed females on the nest increased with female attentiveness (Fig 4A, also *5, 6*) and incubation feeding increased in experimentally parasitized nests (Fig. 4B; $t = 2.2$, $P = 0.02$). However, incubation feeding did not change for parasitized and unparasitized control nests (Fig. 4B; *P*'s > 0.4). Thus increases in attentiveness to protect the nest from egg-removal depended on increased incubation feeding. This increase in activity at the nest comes at a cost; nest predation increases with parental activity such that depredated nests (*24*) had higher incubation feeding rates than successful nests (Fig. 4C). This cost appears robust given that Martin et al. (*7*) found the same costs for other species in a different geographic location.

Yellow Warblers are faced with a trade-off between increasing activity at the nest to defend against cowbird egg-removal versus reducing activity to minimize the risk of predation. This conflict between egg-removal and nest predation appears robust because both egg-removal costs (Fig. 1A, 1C, also see *11*) and nest predation costs from parental activity (*7*) have been documented for a variety of species and locations. Although previously unappreciated, fitness costs of egg-removal are large (Fig 1C, also *4*), and exert strong selection on host parental behavior decisions (Fig. 3A, 3B, 3C, 4B) because of their clear fitness benefits (Fig. 2A, 3D). Yet, these costs and benefits related to egg-removal must be balanced against antagonistic fitness costs from nest predation (Fig. 4C). This antagonistic interaction has gone unrecognized and the optimum solution can vary with the two fitness costs. For example, nest predation strongly constrains incubation feeding across species where parasitism is rare or non-existent (Fig. 5) and incubation feeding is similarly constrained in unparasitized Yellow Warblers where the risk of parasitism is low (gray triangle - Fig. 5). However, egg-removal costs over-ride nest predation constraints on sites where risk of parasitism is high for unparasitized individuals (gray circle), and whenever parasitism has occurred (solid triangle and circle - Fig. 5). These differential responses make sense in the context of Yellow Warbler demography; they are single-brooded in Montana, so a reduction in the number of young lost through egg-removal can not be made up in subsequent nesting attempts. In contrast, loss of the entire nest through predation may be offset by re-nesting after nest failure (*12*). Thus, behavioral responses to immediate risk of parasitism costs may achieve higher priority when risk of parasitism is high. Ultimately, resolution of this antagonistic interaction is a dynamic problem that will vary in time and space among species and populations and deserves more study given its unappreciated consequences for both host fitness and parental care decisions.

References and Notes

1. R. M. May and S. K. Robinson, *Am. Nat.* **126**, 475 (1985); S. K. Robinson, S. I. Rothstein, M. C. Brittingham, L. J. Petit, J. A. Grzybowski, in *Ecology and management of neotropical migratory birds: a synthesis and review of critical issues*, T. E. Martin and D. M. Finch, Eds. (Oxford University Press, New York, 1995).
2. P. E. Lowther, in *Birds of North America*, A. Poole and F. Gill, Eds. (The academy of Natural Sciences, Philadelphia / The American Ornithologist's Union, Washington, DC, 1995), vol. 47.
3. H. W. Hann, *Wils. Bull.* **53**, 211 (1941); D. G. McMaster and S. G. Sealy, *Auk* **114**, 212 (1997).
4. Because single-brooded species only raise one nest to completion, removal of one egg from a successful four-egg clutch reduces seasonal success by 25% and removal of one egg from a successful three-egg clutch reduces seasonal success by 33%.
5. B. E. Lyon and R. D. Montgomerie, *Behav. Ecol. Sociobiol.* **17**, 279 (1985); J. T. Lifjeld and T. Slagsvold, *Anim. Behav.* **34**, 1441 (1986).
6. T. E. Martin and C. K. Ghalambor, *Am. Nat.* **153**, 131 (1999).
7. T. E. Martin, P. R. Martin, C. R. Olson, B. J. Heidinger, J. J. Fontaine, *Science* **287**, 1482 (2000).
8. All study sites are deciduous habitats in Western Montana. See (*9*) for a description of study sites and monitoring methods.

9. J. J. Tewksbury, S. J. Hejl, T. E. Martin, *Ecology* **79**, 2890 (1998).

10. From 1995 to 1999, 57% of 466 Yellow Warbler nests were parasitized.

11. We intensively monitored a subset of 63 Yellow warbler nests to determine the existence and timing of egg-removal. Of 37 parasitized nests, 86% had eggs removed, and many lost multiple eggs (avg 1.32 ± 0.13 eggs lost per nest), while 23% of 26 unparasitized nests lost eggs (avg 0.31 ± 012 eggs lost per nest). Virtually all egg-removal is likely attributable to cowbirds, as removal of less than the entire clutch by predators (partial predation) is very rare on our sites. Moreover, we only found 3 cases of egg-removal in 1,257 nests of species that are rarely parasitized by cowbirds. Finally, we have documented many instances of cowbirds removing natal eggs using video cameras.

12. Yellow Warblers attempted up to 8 nests in a season, with 73% of pairs nesting more than once in a season (n = 460 pairs from 1995 to 1999).

13. We recorded a total of 40 visits by cowbirds from 1997 through 1999 at 132 nests using video cameras, with an average of 18 hours of video per nest during building, laying, and incubation. Video cameras were placed a minimum of 5 m from the nest, covered with camouflage hoods and operated for a minimum of 6 hours, starting before 05:00 MST during building and laying, and before 06:00 MST during incubation.

14. Cowbirds laid eggs in the nest during all visits before 05:30 MST (n = 10), and they were successful in egg-laying regardless of the presence of the female Yellow Warbler on the nest. We considered cowbird visits occurring after 06:00 as

attempted natal egg removal (n = 30), as egg-laying happens exclusively in the very early morning in all populations studied, while egg-removal takes place throughout the day (D. M. Scott, *Can. J. Zool.* **69**, 2093(1991); S. G. Sealy, *Condor* **94**, 40(1992)).

15. H. W. Hann, *Wils. Bull.* **53**, 211 (1941); S. I. Rothstein, J. Verner, E. Stevens, *Ecology* **65**, 77 (1984); D. F. Sherry, M. R. L. Forbes, M. Khurgel, G. O. Ivy, *Proc. Nat. Acad. Sci. USA* **90**, 7839 (1993).

16. We video-taped 5 different cowbird females physically dragging Yellow Warbler females off the nest to allow the cowbird to lay her egg. Both the male and female Yellow Warblers resist these efforts, and it often took the cowbird multiple attempts to remove the female, but in all cases, the cowbird was ultimately successful.

17. S. Rohwer and C. D. Spaw, *Evol. Ecol.* **2**, 27 (1988); S. G. Sealy, *Condor* **94**, 40 (1992).

18. Tests for effects of parasitism risk, nest temperature and predation risk on attentiveness were performed using Pearson's Correlation Coefficients after checking for partial correlations. Temperature at each nest was recorded by placing thermisters of StowAway™ temperature loggers within 2m of each nest. Temperature was recorded every 30 sec., and averaged over the 5-hour time in which attentiveness was recorded. Nest predation during incubation (n = 576 nests) was determined on each of the eight sites using the Mayfield Method (G. L. Hensler and J. D. Nichols, *Wils. Bull.* **93**, 42 (1981)).

19. We had three treatments and nests of all treatments were video-taped from 06:00 until 11:00 am MST on the first full day of incubation (pre-treatment) and on the fourth day of incubation (post-treatment) in a randomized block design. Two nests in each block were initially unparasitized and one nest was naturally parasitized. For our artificial parasitism treatment, we played 10 minutes of cowbird vocalizations and replaced one natal egg with a warmed non-viable cowbird egg at an unparasitized nest one day after the pre-treatment video to simulate parasitism and control for egg-number. Cowbird vocalizations brought cowbirds to the nest area, but cowbirds did not lay eggs or remove natal eggs. For our unparasitized control treatment, we played 10 minutes of Gray Catbird (*Dumetella carolinensis*) song and picked up and replaced one natal egg to control for disturbance at the nest. Catbird vocalizations were chosen because Catbirds are common on our sites and they are similar in size and call volume to cowbirds, but do not represent a threat to Yellow Warblers. Our naturally parasitized treatment recorded behavior using the same pre- and post-treatment videos, but were not visited in between these two video events. We used one-sample t-tests against the null hypothesis of no change in behaviors between pre- and post-treatment videos for all tests.

20. Attentiveness was not related to clutch size across 31 unparasitized nests (ANOVA, $P = 0.788$). Moreover, to test possible clutch volume effects, we removed a natal egg in 8 unparasitized nests, and the cowbird egg in 6 parasitized nests, to compare attentiveness before and after removal. These nests showed no change

in attentiveness (paired t-tests, P's > 0.7).

21. We monitored a total of 3073 nests of 75 species from 1995 through 1999. In this analysis, we included only those nests with a known clutch size that survived past the first day of incubation. Differences in natal clutch size are assumed to be due to removal by cowbirds. This assumption is supported by our more detailed examination of removal in Yellow Warbler nests (*11*), and also in S. I. Rothstein *Am. Nat.* **109**, 161(1975), and S. G. Sealy, *Condor* **94**, 40 (1992).

22. Food allocation was measured on 28 parasitized Yellow Warbler nests. Video observations were taken from 06:00 to 12:00 MST on day 3-5 of the nestling period. All nests had 1 cowbird nestling and 1 (n = 8), 2 (n = 8), 3 (n = 10), or 4 (n = 2) natal young.

23. Attentiveness (percent of time on the nest) was measured on day 4 of incubation (*13*) and averaged for each site. Parasitism for each site was determined using daily parasitism rates for Yellow Warblers raised to the 7 day period length over which cowbird eggs are typically laid [see C. M. Pease and J. A. Grzybowski, *Auk* **112**, 343 (1995)]. Data for parasitism include a total of 369 nests, and data for incubation feeding and attentiveness are from 32 unparasitized nests.

24. Incubation feeds and total trips to the nest were measured on day 5 of incubation from 06:00 to 11:00 MST (*13*). Nests were considered successful if they survived from the time of the video through the third day of the nestling period. We used this period because females brood nestlings during the early nestling period and their attentiveness is dependent on male feeding through this time. P-

values are ANOVA tests between failed and successful nests.

25. We thank Todd Ondick and Todd Musci for field assistance, and Paul Martin, and John Lloyd for helpful comments. We are grateful to the Bitterroot National Forest for logistical support. This work was supported by a grant from the National Science Foundation (Dissertation Improvement Grant IBN-990212), and the Bitterroot Ecosystem Management Research Project, Rocky Mountain Research Station, Forestry Sciences Laboratory, Missoula, Montana.

Figure Legends

Fig. 1. (A) Mean clutch size was reduced by an average of 0.85 eggs in parasitized nests (gray bars) compared to unparasitized nests (black bars) (ANOVA $F = 65$, $P < 0.0005$) across all species parasitized on our sites in Montana (*21*). Sample sizes for unparasitized/parasitized nests, respectively, are in parentheses. (B) In Yellow Warbler nests, the rate (feeds per hour) of feeding cowbird young (*22*) increased as the number of natal young decreased (ANOVA $F = 65$, $P < 0.0001$). (C) Parasitized Yellow Warblers fledge less young per successful nest when they have fewer natal eggs in the clutch ($r = 0.56$, $P = 0.002$, $n = 27$), demonstrating a fitness cost to natal egg-removal by cowbirds.

Fig. 2. (A) The success of cowbirds at laying parasitic eggs (laying) was not influenced by presence of the female Yellow Warbler on the nest (Likelihood ratio test $G = 171$, $P < 0.0005$). However, the success of cowbirds in removing natal eggs (removal) was drastically reduced when the female Yellow Warbler was present on the nest (black bars) compared to times when she was absent (gray bars). (B) The daily chance that a natal egg is removed in parasitized nests increases dramatically immediately after the nest is parasitized (shift from light gray bars to dark gray bars), when probability is highest and closely follows a log-normal distribution (curve = non-linear regression $r^2 = 0.87$, $n = 47$, $P < 0.0001$).

Fig. 3. (A) Attentiveness (percent of time on the nest) of unparasitized nests increases

with the overall rate of parasitism ($r = 0.93$ $P = 0.0005$) across 8 sites (*23*). Triangles are sites used in Fig 3B as low parasitism sites, circles are high parasitism sites. (B) Attentiveness (percent time on the nest) was lower in areas with low parasitism risk (ANOVA $F = 10.4$, $P = 0.002$; triangles in Fig 3A) and lower in unparasitized nests (ANOVA $F = 8.9$, $P = 0.004$; gray bars). However, the difference in attentiveness between parasitized and unparasitized nests was much greater in areas of low parasitism risk. (C) Attentiveness increased significantly after experimental parasitism (gray bars), but remained unchanged in unparasitized control nests (white bars), and parasitized control nests (black bars), in a randomized block experiment, showing that Yellow Warblers do increase attentiveness when parasitized. Change in attentiveness represents the difference between pre-treatment and post-treatment measurement of attentiveness (see *19*). (D) Attentiveness (mean ± 1 SE) for naturally parasitized nests was significantly lower ($t = 2.5$, $P = 0.01$) in nests where an egg was removed (YES) than in nests where an egg was not removed (NO), thus increased attentiveness reduces risk of egg-removal.

Fig. 4. (A) Incubation feeding rate (trips per hour that males made to the nest to bring food to the female) was highly correlated with attentiveness ($r = 0.77$, $P < 0.001$; filmed at day 4 of incubation, n = 63 nests). (B) Incubation feeding increased significantly after experimental parasitism ($t = 2.6$, $P = 0.01$; gray bars), but remained unchanged in unparasitized control nests (white bars), and

parasitized control nests (black bars), in the same randomized block experiment as in Fig 3C. Change in attentiveness represents the difference between pre-treatment and post-treatment measurement of incubating feeding rates (see *19*). (C) Incubation feeding rate (Mean ± 1 SE) was significantly lower for nests successful during incubation than for those depredated during this period ($t = 2.6$, $P = 0.01$, *24*).

Fig. 5. (A) Species without risk of parasitism (open squares) exhibit reduced rates of incubation feeding (trips per hour that males made to the nest to bring food to the female) with greater risk of nest predation (n=18 species from Arizona and Montana, see *6*). Unparasitized (light gray triangle) nests of Yellow Warblers on sites with low risk of parasitism (see Fig. 3) fit the relationship closely. However, parasitized (solid triangle) yellow warbler nests from plots with low risk of parasitism and both unparasitized (gray circle) and parasitized nests (solid circles) on plots with high risk of parasitism (see Fig. 3A) show incubation feeding behavior that is elevated above the rate expected by the evolutionary constraint of predation (dotted line). Thus, potential immediate costs of egg loss from egg-removal following parasitism or in high risk areas over-rides constraints of nest predation.

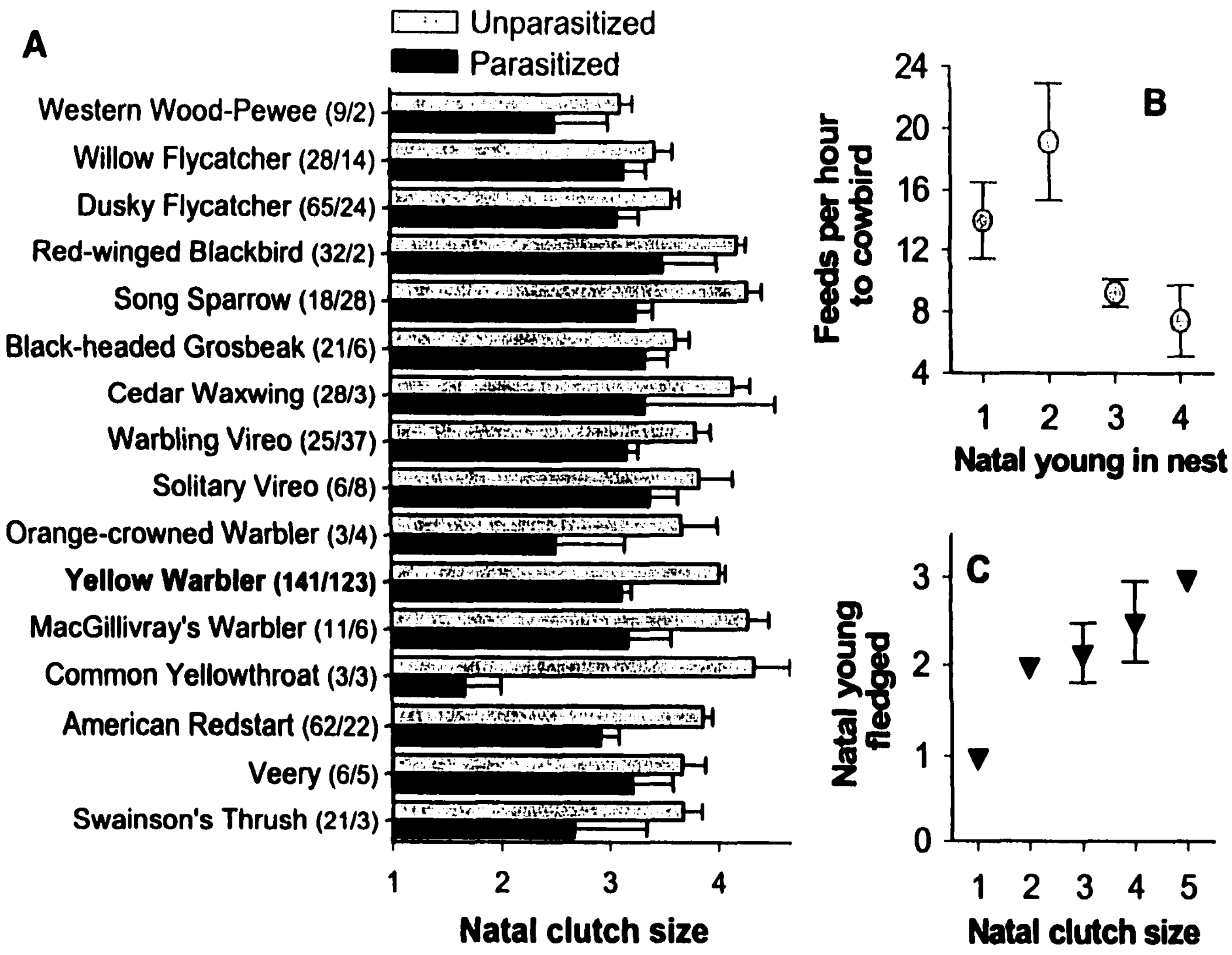
A
Unparasitized
Parasitized
Western Wood-Pewee (9/2)
Willow Flycatcher (28/14)
Dusky Flycatcher (65/24)
Red-winged Blackbird (32/2)
Song Sparrow (18/28)
Black-headed Grosbeak (21/6)
Cedar Waxwing (28/3)
Warbling Vireo (25/37)
Solitary Vireo (6/8)
Orange-crowned Warbler (3/4)
Yellow Warbler (141/123)
MacGillivray's Warbler (11/6)
Common Yellowthroat (3/3)
American Redstart (62/22)
Veery (6/5)
Swainson's Thrush (21/3)
1
2
3
4
Natal clutch size
B
Feeds per hour to cowbird
24
20
16
12
8
4
1
2
3
4
Natal young in nest
C
Natal young fledged
3
2
1
0
1
2
3
4
5
Natal clutch size

Figure 1

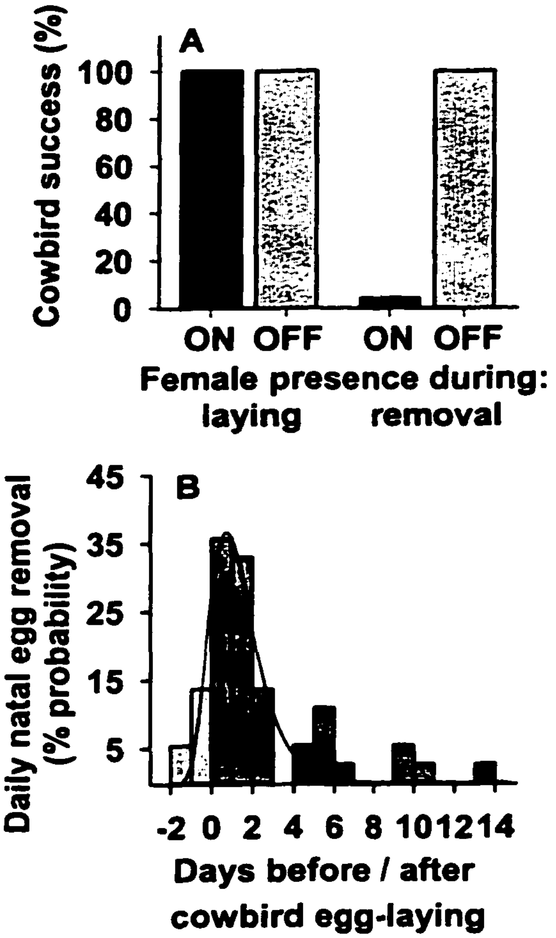
A
Cowbird success (%)
100
80
60
40
20
0
ON
OFF
ON
OFF
Female presence during:
laying
removal
B
Daily natal egg removal
(% probability)
45
35
25
15
5
-2
0
2
4
6
8
10
12
14
Days before / after
cowbird egg-laying

Figure 2

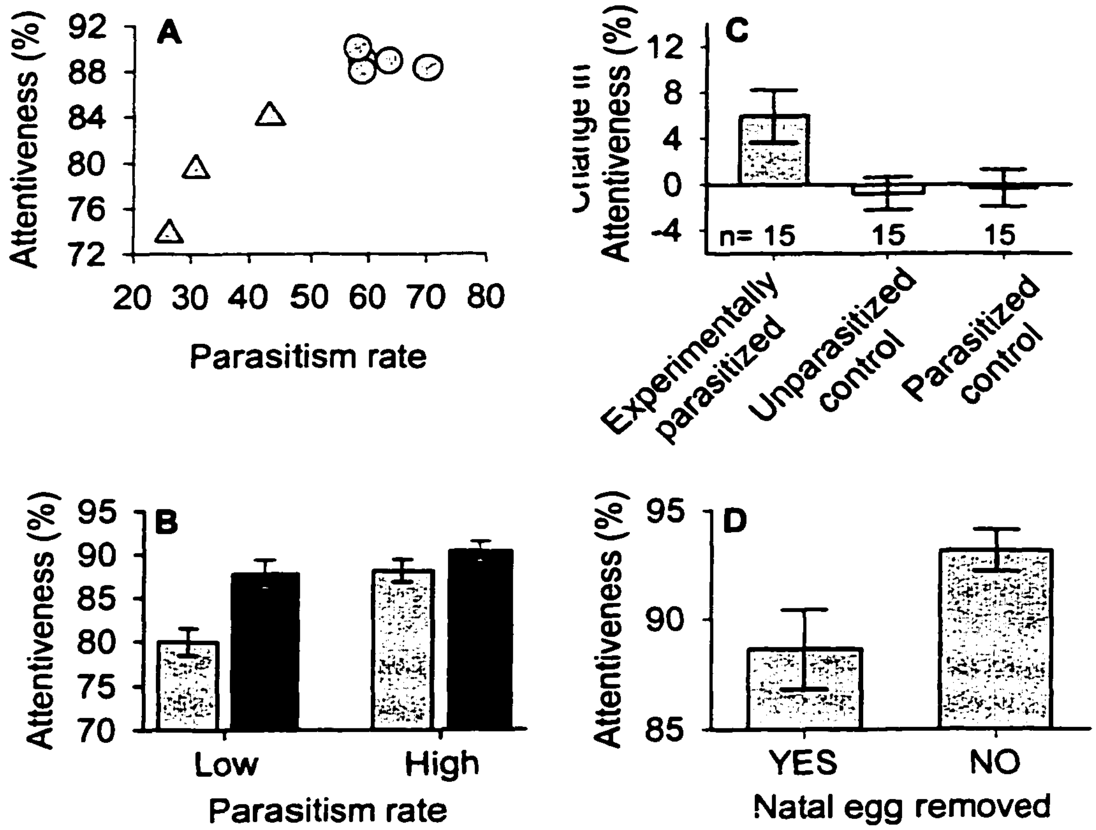
A
Attentiveness (%)
92
88
84
80
76
72
20 30 40 50 60 70 80
Parasitism rate
C
Attentiveness (%)
12
8
4
0
-4
n= 15
15
15
Experimentally parasitized
Unparasitized control
Parasitized control
B
Attentiveness (%)
95
90
85
80
75
70
Low
High
Parasitism rate
D
Attentiveness (%)
95
90
85
YES
NO
Natal egg removed

Figure 3

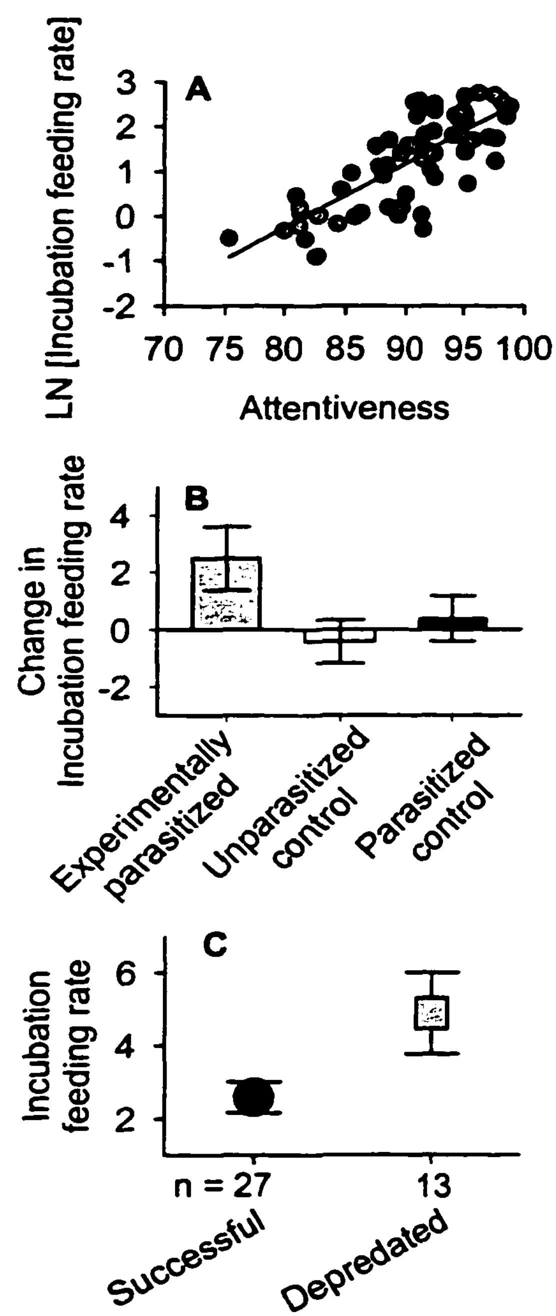
A
LN [Incubation feeding rate]
3
2
1
0
-1
-2
70 75 80 85 90 95 100
Attentiveness
B
Change in Incubation feeding rate
4
2
0
-2
Experimentally parasitized
Unparasitized control
Parasitized control
C
Incubation feeding rate
6
4
2
n = 27
13
Successful
Depredated

Figure 4

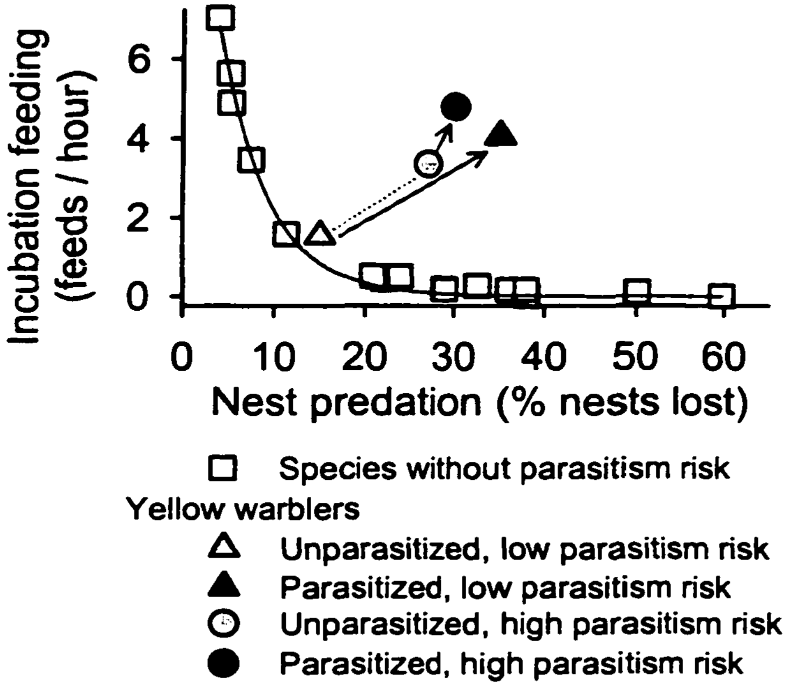
Incubation feeding
(feeds / hour)
0
2
4
6
0
10
20
30
40
50
60
Nest predation (% nests lost)
□ Species without parasitism risk
Yellow warblers
△ Unparasitized, low parasitism risk
▲ Parasitized, low parasitism risk
○ Unparasitized, high parasitism risk
● Parasitized, high parasitism risk

Figure 5

Chapter 5

Brood parasitism, nest predation, and the importance of life history differences between Neotropical Migrants

Abstract

The annual fecundity of passerine birds is dependant on the life-history of the species and the rate of nest failure and brood reduction encountered, and the two primary causes of nest failure and brood reduction across most passerines are nest predation and brood parasitism. However, the interactions between life-history, nest predation and brood parasitism have not been explored in a demographic context. We examined the demographic effects of different levels of nest predation and brood parasitism in two Neotropical migrant species, American Redstart (*Setophaga ruticilla*) and the Yellow Warbler (*Dendroica petechia*), that differ in clutch size, nestling fledging success (the percentage of the clutch that fledges) and the rate at which birds re-nest following nest failure in two single-brooded Neotropical migrant passerines. We used data on density, breeding success and adult survival collected over five seasons in deciduous forests in western Montana to construct a daily model estimating seasonal fecundity and population growth of each species. We used results from this model to examine the relative importance of different life-history parameters in determining differences in seasonal fecundity between these two species. Under current levels of nest predation and brood parasitism, Yellow Warblers produced 1.52 young per female per season and American Redstarts only 0.99 young per female per season, too few young to balance mortality. However, only American Redstarts show declines in population size. Our analysis suggests that seasonal differences in clutch-size reduction and re-nesting rates both have a large effect on the difference in seasonal fecundity between these species. Further, while both nest predation and brood parasitism limit seasonal fecundity for both species, American Redstarts are more limited by nest predation, regardless of levels of brood parasitism, while Yellow Warblers are more limited more by brood parasitism in this situation, but would become more limited by predation if parasitism was lower than 40%.

These results suggest that incorporating detailed examinations of life history into population models will yield more precise estimates of the demographic effect of nest predation and brood parasitism.

Key Words: Nest predation, brood parasitism, demography, life-history, *Setophaga ruticilla*, *Dendroica petechia*.

Introduction

Declining populations of many migratory and resident bird species has generated intense concern and debate about the causes of decline (Hagan and Johnson 1992, Jehl and Johnson 1994, Martin and Finch 1995, Newton 1998). On the breeding grounds, much research has focused on the effects of forest fragmentation (Robinson et al. 1995a, Donovan et al. 1997, Tewksbury 1998) while in the tropics, ecologists examine the potential role of wintering ground habitat destruction (Robbins et al. 1989, Terborgh 1989, Rappole and McDonald 1994, Sherry and Holmes 1996). Recent work has now begun to link process between breeding and wintering grounds (Marra et al. 1998). The two processes causing the largest demographic effects on the breeding grounds are nest predation and brood parasitism, together accounting for as much as 90% of nest failures (Martin 1992). Yet the relative importance of these processes has received attention only recently (Brawn and Robinson 1996, Schmidt and Whelen 1999, Woodworth 1999), and there has been no clear documentation of the interaction between nest predation and brood parasitism across different avian life histories.

High levels of nest predation and brood parasitism have clearly contributed to population decline in certain species (Mayfield 1961a, Post and Whiley 1977, Goldwasser et al. 1980, Trail and Baptista 1993,Woodworth 1997, Kus 1999), but to date, studies clearly identifying the relative costs of nest predation and brood parasitism on seasonal fecundity have been conducted only on single species (King and Mewaldt 1987, Trail and Baptista 1993, Pease and Grzybowski 1995, Woodworth 1999) and due to differences in data collection and analysis, comparisons across species have not been attempted. Recent models by Pease and Grzybowski (1995) and Schmidt and Whelan (1999) suggest that differences in a number of breeding season life history variables may have large effects on the demographic impact of brood parasitism and nest predation.

We compared the life-histories of two Neotropical migrant species, the American Redstart (*Setophaga ruticilla*) and Yellow Warbler (*Dendroica petechia*), breeding in the same river valley in Western Montana to determine the relative importance of different life-history traits in influencing the demographic costs of nest predation and brood parasitism by the Brown-headed Cowbird (*Molothrus ater*). We use breeding season data and survivorship estimates of banded birds collected over 5 years to determine differences in the effect of brood parasitism and nest predation on the reproductive success of these species. We then construct a model to estimate seasonal fecundity based on our findings, and use our estimates of seasonal fecundity to estimate population growth rates (λ) for each species. We use results from this model to ask the following questions: 1) At what level of brood parasitism could these species maintain stable populations under current levels of nest predation? 2) how important are differences in clutch size, fledging success, and re-nesting rates in determining seasonal reproductive success and population growth of these species under the full range of parasitism rates possible? and 3) given that brood parasitism and nest predation act in very different ways on seasonal fecundity (Pease and Gryzbowsk 1995, Schmidt and Whalen 1999, Woodworth 1999), how important are each of these processes in determining population health?

Methods

Study area

Populations of American Redstarts and Yellow Warblers were monitored on 16 study sites in riparian habitat in western Montana. Redstarts were found primarily in riparian areas in the foothills of the Bitterroot Mountains (8 sites) while Yellow Warblers were the most abundant species in deciduous forests bordering the Bitterroot River (8 sites). We restricted our analysis to Yellow Warblers in the valley bottom sites (91% of all pairs monitored) due to potential differences in re-nesting rates in foothill study sites and the low numbers of nests in those habitats. American Redstarts showed no differences in re-nesting rates between habitats, so we included all American Redstart pairs. A full description of the study sites can be found in Tewksbury et al. (1998 - chapter 1).

Field methods

We monitored the abundance, density, breeding success and annual return rates of American Redstarts and Yellow Warblers from 1995 - 1999 through intensive territory mapping and nest monitoring coupled with a banding, resighting and recapture effort focused exclusively on these two species. To determine period lengths, clutch sizes, parasitism rates, nesting success and fledging success (% of clutch fledged) we monitored a total of 139 American Redstart nests from 95 nesting pairs and 814 Yellow Warbler nests for 498 nesting pairs following the BBIRD protocol (Martin et al. 1996). We used tree-climbing ladders and 10m nest poles to check clutch sizes, hatching success, period lengths and parasitism. We were thus able to monitor nests at all nest-heights. Each year, we checked a subset of nests of each species each day or every other day to obtain more accurate data on the timing of parasitism and period lengths and reduce estimation error for these parameters (Pease and Grzybowski 1995).

To determine female abundance and track females through multiple nesting attempts, we mapped each breeding territory, banded both males and females of as many pairs as possible (on average 85% of American Redstart and 69% of Yellow Warbler pairs had either the male or female banded) and focused nest-searching on finding re-nests after nest failure. We were able to track re-nests with a high degree of accuracy due to banded birds, and because re-nesting females almost always started their new nest within 1 – 3 days of the previous nest failure, within 50m of their previous nest (in the same territory), and with the same male. Detailed data on nest history was kept for each pair to determine the total number of nesting attempts, and the date each pair started and terminated nesting. The traditional approach to determining average seasonal fecundity is to use only those pairs for which all nesting attempts were monitored, and divide the total number of young fledged by the number of females (Nolan 1978). However, both species are single-brooded in our populations, thus they do not re-nest after a successful attempt (whether they fledged their own young or a Brown-headed Cowbird). Because it is a much simpler task to find all the nests of pairs that fledge young during their first attempt than it is to find all the nests of pairs that fail multiple times throughout the season, estimates of seasonal fecundity may be strongly biased, inflating the average seasonal fecundity of the population. Alternatively, using all pairs causes an underestimate of seasonal fecundity, because it includes pairs which might have re-nested successfully, but whose final nest was not found. However, because both species either re-nested or left the territory soon after nest failure, it is a much simpler task to determine when a pair stops nesting after failure of a previous nest, and when they re-nest, regardless of the number of nesting attempts they have undertaken. Re-nesting is strongly dependant on the period within the season, as birds stop re-nesting prior to departing the breeding grounds, and we can thus model re-nesting probability as a function of the period within the nesting season in which the previous nest failed, and estimate seasonal fecundity by linking seasonal changes in clutch size, nest predation, and brood parasitism to re-nesting probability.

Because all non-breeding individuals found were males, our estimates of abundance are based on all female territories. To determine apparent annual survival, continuous resighting was undertaken throughout the breeding season both on and near each study site. In 1998 and 1999, additional resighting was conducted in Yellow Warbler habitat between study sites to determine the number of banded birds that returned to breed off of our sites.

Demographic modeling

To assess the impact of brood parasitism and nest predation we constructed a seasonal fecundity model using Stella 5.1.1 (High performance Systems inc. 1998) and applied a basic stage-based matrix model to estimate population growth rates. Our seasonal fecundity model is conceptually similar to earlier models established for passerines (Pease and Grzybowski 1995, Woodworth 1999), being a daily model that tracks females from the time they initiate breeding in the season through multiple breeding attempts until she successfully fledges at least one young or does not re-nest following nest failure (Fig. 1). However, our model is more closely related to the detailed model of Pease and Gryzbowski (1995) as it can accommodate seasonal changes in all parameters, including changes in clutch size, levels of brood reduction, re-nesting probability, nest predation and brood parasitism. The start of the breeding season was defined as the day in which 50% of females had begun building their first nests. This value varied across years (ANOVA $F = 36.1$, $P < 0.0005$) and by species (ANOVA $F = 11.0$, $P = 0.001$) due to differences in vegetation phenology and the dates at which birds return to the breeding grounds (American Redstarts begin nesting an average of four days after Yellow Warblers). Thus the distribution of breeding start dates was determined separately for each species. However, we found that many aspects of the breeding biology of these species, such as re-nesting probability and clutch size (see below) were conditional on the day within the breeding season. Thus we standardized all dates across all years as a function of the median date of first nest initiation within a particular season (season date = 0) for each species. We then used year as a factor in initial tests of life-history parameters, to determine if annual variation played a role beyond the shift in the start of the breeding season.

Females start nesting according to the distributions of season days (*Sd*) in which females begin building their first nest (Fig. 1), with a median of $Sd = 0$, as we standardized start dates among years (above). For both species, start dates were normally distributed (Table 1; K-S Z's < 1.4, P's > 0.05 for both species). As most breeding season parameters varied as a function of whether a nest was parasitized or not, separate nesting cycles are defined for parasitized and unparasitized nests. Females enter the unparasitized or parasitized nest cycle in relation to the fraction of nests parasitized (P_P), which can vary throughout the season (see below). Within the nest cycle, daily nest success rates (*ds*) for each period (building, egg-laying, incubation, and nestling stages) are raised to the length of each period to produce a Mayfield adjusted probability that a nest survives the period (Fig 1B). Females whose nests survive the period move to the next period, and eventually fledge young if they are successful. The number of young a female fledges is a product of her initial clutch size (*Cs*) and the percent of the clutch that fledges (P_F). Females that fail may nest again (P_{RN}, Table 1), beginning the second nesting attempt (Fig. 1C). This process continues until all females stop re-nesting. Seasonal fecundity is thus the average number of young fledged per female in the season.

We used our estimates of seasonal fecundity in a basic two-stage matrix model (Fig. 2) to generate an estimate of population growth rate (λ). We use a female-based model because females appear to be the limiting sex in both species, as the only non-breeding floaters found for either species were males. We did not differentiate between the fecundity (*F*) of first year birds and older birds (thus $F_1 = F_2$) because juvenile birds were not banded, thus the age of many newly banded birds was not conclusively determined. Adult survival (P_2) was determined using program Mark (White and Burnham 1999). We used four estimates of juvenile survival (P_1) to capture the full range of possible juvenile survival for passerines (See survival estimation, below).

Breeding season life history and nest predation

To parameterize the seasonal fecundity model, we examined brood parasitism and nest predation, as well as each life-history trait, for seasonal dependence, differences between parasitized and unparasitized nests, and for relations between traits (Table 1).

Calculating brood parasitism and nest predation rates

Observed rates of brood parasitism are confounded with nest predation pressure, because as nest predation increases, nests are more likely to be predated before the end of the window when parasitism can occur (Pease and Grzybowski 1995), reducing the observed parasitism rate without changing parasitism pressure. Additionally, when birds frequently abandon parasitized nests, the observed rate of parasitism will be lower than actual parasitism, because parasitized nests are more likely to be abandoned in building and early egg-laying, often before they are found. This results in an undercounting of parasitized nests. Further confounding this problem, many studies following Mayfield's protocol to assess nest success (Mayfield 1961b, 1975; Hensler and Nichols 1981) do not consider nests that fail before the day the first natal egg is laid (but see Pease and Grzybowski 1995, Woodworth 1999), yet in many passerines, nests that are parasitized during building are much more likely to abandon before clutch initiation than unparasitized nests (Biermann et al. 1987, Pease and Grzybowski 1995, Sealy 1995, Braden et al. 1997, Rogers et al. 1997, Kus 1999), resulting in a further undercounting of parasitized nesting attempts.

To account for these biases, we report standard rates of parasitism (Pease and Grzybowski's cohort parasitism) as observed parasitism, and we also develop a modified Mayfield method (Mayfield 1961b, 1975; Hensler and Nichols 1975) to calculate daily parasitism rates and actual parasitism pressure – the chance that a nest will be parasitized if it survives throughout the window in which parasitism occurs. Unlike observed parasitism, this metric is independent of predation rate, and accounts for the number of days each nest is actually available to be parasitized. The Mayfield method applied to parasitism simply sums the number of days each nest was exposed to parasitism across all nests, and counts the number of nests that are parasitized within this window. The sum of all exposure days divided by the number of nests parasitized gives a daily probability of an unparasitized nest becoming parasitized (Pease and Grzybowski 1995). The accuracy of daily parasitism is contingent on the assumption that the daily chance of parasitism does not vary greatly within the period of exposure (Hensler and Nichols 1981). In our study species, 97% of the all parasitism events, and 100% of parasitism events where the cowbird hatched, took place from the last day of building through the second day of incubation (Fig. 3A and 3B), thus the window for parasitism is approximately 8 days long. However, the daily chance of parasitism varies greatly within this window (Fig 3); over 50% of all parasitism occurs on the second day of egg laying, while less than 5% of parasitized nests are actually parasitized on any day after the 4th day of egg laying. Thus, an unparasitized nest which is depredated four days after clutch initiation has escaped almost all chance of being parasitized, while an unparasitized nest that is depredated on the day of clutch initiation was unavailable for parasitism during the period when over 75% of the parasitism occurs. To account for this variation in parasitism across the period of exposure, we weighted each exposure day by the proportion of parasitism that occurs on that day (Fig 3). Parasitism rates did not vary significantly among the years of the study for either species (American Redstart $\chi^2 = 1.2$, $df = 3$, $P = 0.76$; Yellow Warbler $\chi^2 = 3.1$, $df = 4$, $P = 0.54$), thus all years were combined for analysis.

We found that the incidence of multiple parasitism was much less common than parasitism itself. Observed parasitism was 37% for American Redstarts (n = 126), and 61% for Yellow Warblers (n = 397), while multiple parasitism occurred in 22% of parasitized nests in both species. Because multiple parasitism was comparatively uncommon, we were unable to clearly separate the effects of multiple parasitism versus single parasitism on nest failure rates, clutch size reduction, and fledging success in both species. We therefore present parameters for parasitized nests including nests parasitized multiple times and accordingly, our estimates of observed parasitism and parasitism pressure represent the risk of an unparasitized nest becoming parasitized regardless of whether it is parasitized a second time. This methods accounts for double parasitism by including these nests in our estimates of the effect of parasitism, and because multiple parasitism did not vary by species ($\chi^2 = 0.71$ $P = 0.4$) or with season day ($t = 1.4$, $P = 0.15$), this method is unlikely to bias our model results.

We calculated daily survival (*ds*) rates for each nesting phase of both species using the Mayfield Method (Mayfield 1961b, 1975; Hensler and Nichols 1975). Nests were considered successful if they fledged 1 or more of their own young, nests that only fledged cowbirds were considered failed on the day the last natal young died, or the predicted hatch date if no natal young hatched. To test for a seasonal effect on nest predation, we grouped nests into 8 day blocks based on the season day in which the nest was initiated. We combined nests across years and calculated daily survival rates for all phases of the nesting cycle (building, egg laying, incubation, and nestling phases). We then used program Contrast (Sauer and Williams 1989) to test for differences in daily predation rates across the season and between species.

Clutch size, period lengths, fledging success, and re-nesting

We used general linear models to examine the effects of species, parasitism, the nest attempt number, the day within the season the nest started (season day), and year on building time, clutch size, and the length of the incubation and nestling periods. Nest attempt and season day were treated as covariates in these models. We tested for the same factors when examining fledging success (P_F), but also included clutch size, as a smaller percentage of young may be fledged from larger clutches.

We predicted that the probability of a female re-nesting following nest failure would be a function of the season day of the previous nest failure, and that this function would differ by species. To test this prediction, we used logistic regression, first running a model with just these two factors included, and then running a full model which included these variables plus nest attempt number, as well as parasitism and clutch size of the previous nest. We then compared the classification rates and Log Likelihood scores of both models and significance of the different variables in the full model. In addition, we ran both forward and backward stepwise models using the

Likelihood Ratio technique for addition and deletion of variables to test the agreement of our predicted model with stepwise models.

Apparent survival

The Cormack-Jolly-Seber (CJS) suite of models (Program MARK, White and Burnham 1999) were used to estimate apparent survival (Phi) and detection probability (P) for American Redstarts and Yellow Warblers based on five seasons of banding and resighting. We determined *a priori* a candidate set of models based on the biology of each species and the questions of interest (Burnham and Anderson 1998). This candidate set included variations in time and between groups (sex). For fully time-dependent models, Phi and P are confounded in the final year of resighting, and this can limit the amount of useable information from the final season. In an effort to take full advantage of the extra Yellow Warbler resighting effort in 1999, for this species we split the final year into two time periods. Thus the first half of 1999 provided unconfounded parameter estimates such that both survival and detection could be estimated (M. Lindberg, pers. comm.).

The best approximating model was chosen based solely on Akaike's Information Criterion (AICc). This approach determines which model best explains the variation in the data while incorporating the fewest parameters, thus balancing fit and precision (Burnham and Anderson 1998). The model with the lowest AICc value was considered the best approximating model and inference was based on these estimates and 95% confidence intervals. Apparent survival cannot distinguish between permanent emigration and mortality, thus our estimates are minimum estimations of actual survival. We used estimated survival from the best models for each species as the low estimation, and we used the high 95% confidence intervals as high survival estimates. In addition, where even our high estimates are lower than those previously published, we use the published survival estimates as an alternative survival estimate.

Survival from hatch through the first year (juvenile survival, P_1 of Fig. 1B) is poorly understood for passerines, and previous models have used an estimation of 31% annual survival for juveniles or 50% of adult survival across many species (Ricklefs 1973, Greenberg 1980, Temple and Carey 1988, Donovan et al. 1995). To capture the full range of possible juvenile survival, we ran models with juvenile survival set from 40% to 70% of adult survival. The upper end of this range is highly optimistic, as Juvenile survival includes mortality in the post-fledging phase, when young birds are less mobile and are learning to forage.

Models and questions

To address our first question concerning the maximum level of parasitism under which these populations are likely to remain stable ($\lambda >= 1$) under current levels of nest predation, we estimated seasonal fecundity under observed rates of brood parasitism and nest predation, and modeled population growth (λ) across the range of adult and juvenile survival values for each species. We compared these results to trends in the number of breeding pairs on our study sites over the five years of study. While a constant population size does not necessarily mean that a population is sustainable (Van Horne 1983), the rate of population decline may provide an independent measure of local λ, which can be compared to predicted values based on our demographic data. We also ran models from 0% to 100% parasitism for both species using the four levels of juvenile survival, and generated $\lambda = 1$ isoclines as functions of adult survival, allowing us to determine the level of adult and juvenile survival needed for stable population growth, given our estimations of seasonal fecundity for each species.

To determine the relative importance of differences in clutch size, fledging success, and re-nesting rates between these species, we ran a series of models over the full range of parasitism for each species, and swapped the values of one life-history parameter at a time between the species. We then calculated the change in seasonal fecundity when compared to null models (in which all parameters were set at the rates for that species). Finally, to address the relative importance of nest predation vs. brood parasitism, we ran an additional series of models across the full range of parasitism with a 10% reduction in daily predation rates across all nesting stages in both parasitized and non-parasitized nests, and then a 10% decrease in daily parasitism pressure across this same range. This decrease in daily nest predation and daily parasitism represents the expected effect of removing 10% of the nest predators or cowbirds from the landscape, assuming no functional responses of remaining predators or cowbirds.

We used general linear models to test for the effects of all possible effects on each parameter, reducing models to exclude non-significant interactions and main effects. Results for all significant effects in the final models are reported, as well as excluded variables where appropriate. We included all effects explaining a substantial amount of variance ($P < 0.15$) in final models.

Results

Life-history parameters

Nest building time did not differ between the species ($F = 1.4$, $df = 1, 46$, $P = 0.244$), parasitism, ($F = 0.3$, $df = 1, 46$, $P = .617$) or initiation date ($F = 0.74$, $df = 1, 46$, $P = 0.770$), but was strongly affected by nest attempt number ($F = 4.4$, $P = 0.004$) because nest building time was much shorter after the first attempt (Table 2). Clutch size differed between species ($F = 6.4$, $df = 1, 350$, $P = 0.011$) and was affected by brood parasitism (Fig. 4; $F = 109$, $df = 1, 350$, $P < 0.001$). Clutch size averaged 3.8 eggs for unparasitized American Redstarts, with an average clutch reduction of 0.94 eggs (24%) in parasitized nests. Clutch size averaged 4.0 eggs for unparasitized Yellow with an average clutch reduction of 0.90 eggs (22%) in parasitized nests. This reduction in clutch size is entirely attributable to cowbirds removing natal eggs (Tewksbury et al, in prep – chapter 4). Season-day also strongly affected clutch size ($F = 20.6$, $df = 1, 350$, $P < 0.001$), with smaller clutches being laid later in the season, particularly for American Redstarts (Fig. 4). Egg-removal by cowbirds may also vary somewhat across the season, as early and later parasitized nests had large clutch reductions, but nests initiated just after the mean season start date experienced less removal in both species (Fig. 4). The number of previous nesting attempts had no effect on clutch size ($F = 0.3$, $df = 1, 350$, $P = 0.705$). We ran a parallelism test on unparasitized nests to determine if natural clutch size (unaffected by cowbird egg removal) declined at significantly different rates between the two species, and found that clutch size declined more steeply in American Redstarts than in Yellow Warblers (species x initiation day interaction $F =$

5.4, *df* = 1, 350, *P* = 0.021). Even with the substantially reduced clutch size in parasitized nests, American Redstarts and Yellow Warblers both fledged a smaller percentage of the clutch (lower fledging success) when parasitized (Fig. 5), with the effect stronger in American Redstarts (*F* = 12.3, *df* = 1, 34 *P* = 0.001) than in Yellow Warblers (*F* = 5.7, *df* =1, 85, *P* = 0.019). In Yellow Warblers, fledging success also declined as clutch size increased (Fig. 5; *F* = 6.7, *df* =1, 85, *P* = 0.011) regardless of parasitism (clutch size x parasitism interaction *F* = 0.3, *df* =1, 85, *P* = 0.56). Clutch size did not influence fledging success for American Redstarts (*F* = 0.7, *df* = 1, 34 *P* = 0.789).

The probability of a female re-nesting after nest failure differed strongly between the species (P < 0.001 in both the predicted logistic model and the full model), thus we ran separate logistic regressions for each species. Re-nesting was highly dependent on the season day for both species (Fig. 6) and was the only significant variable in full models (Table 3). The shape of the re-nesting curve for the two species differed substantially; the season date in which 50% of American Redstarts stopped re-nesting was 9 days earlier then the date for Yellow Warblers (Fig. 6). If we define the length of the breeding season as the number of days from the day 50% of females initiate nests to the day 50% of the females fail to re-nest following nest failure (Pease and Grzybowski 1995), the breeding season for American Redstarts is 31% shorter for American Redstarts, at 17.5 days, than for Yellow Warblers. In addition to the difference in breeding season length defined by re-nesting, there was greater variation in re-nesting for American Redstarts than Yellow Warblers (Fig. 6). Both forward and reverse stepwise models for American Redstart re-nesting included female nesting attempt along with season date, suggesting that once the season day of the previous nest failure was accounted for, American Redstarts are more likely to re-nest after a failed second attempt than a failed first attempt (*Exp(B)* = 3.7, $P = 0.06$). Stepwise models for Yellow Warblers included clutch size with season date, suggesting that once the season day of the previous failure is accounted for, females with larger clutches re-nest less often (*Exp(B)* = 0.59, $P = 0.043$). However, the number of nests correctly classified when including attempt number with season day increased by less than 3% over the model with season alone for American Redstarts (change in Log-likelihood if attempt number removed = 3.9, P = 0.043), and including clutch size in the Yellow Warbler model yielded no increase in model accuracy (change in Log-likelihood if clutch size removed = 4.2, $P = 0.041$). Thus the additional effects of nest attempt number and clutch size appear small compared to the effect of season day. Therefore, for modeling purposes, we used only the day of failure of the previous nesting attempt to create re-nest functions (Fig. 6).

Parasitism and nest predation

Observed brood parasitism and parasitism pressure were significantly higher for Yellow Warblers than American Redstarts (Fig. 7A; $\chi^2 > 20$, *P*'s < 0.001). American Redstarts had an observed parasitism rate of 37% (n = 127 nests) and a daily rate of parasitism (the average chance of a nest becoming parasitized each day it is exposed to parasitism) of 0.069, yielding a 43% chance of a nests becoming parasitized if it survives throughout the 8-day period when cowbird eggs are laid. Yellow Warblers had an observed parasitism rate of 61% (n = 423 nests), and a daily rate of parasitism of 0.140, yielding a parasitism pressure of 70%. The difference between observed parasitism and parasitism pressure was only significant for Yellow Warblers (Fig. 7A, $\chi^2 = 16$, $P = 0.0001$) due to the lower sample size and smaller differences in American Redstarts (Fig. 7A, $\chi^2 = 1.2$, $P = 0.16$). Parasitism pressure did not vary across the season for Yellow Warblers ($r^2 = 0.19$, $P = 0.24$), but increased as the season progressed for American Redstarts ($r^2 = 0.69$, $P = 0.006$).

Almost all nest mortality was caused by nest predation and brood parasitism (Fig. 8, dark gray and gray areas). Daily nest mortality did not vary by year or season date for either species (χ^2 's < 1.5, P's > 0.3) Within parasitized nests, parasitism was almost completely responsible for the extremely high nest mortality during egg-laying (Fig. 8B), creating large differences between parasitized and unparasitized mortality rates (American Redstart $\chi^2 = 10.2$, $P = 0.001$; Yellow Warbler $\chi^2 = 40.8$, $P < 0.0001$) This nest failure was due to abandonment of parasitized nests, which occurred both in late-building and in the egg-laying stage. In total, Yellow Warblers abandoned 40% of parasitized nests (n = 252), 22% by burying the contents of a previous nest and building a new nest directly over the old one, and 18% by abandoning the nest entirely. American Redstarts abandoned 37% of parasitized nests (n = 48), and we recorded only one case of a Redstart burying a clutch and starting a new nest on top.

Total daily mortality tended to be higher in parasitized nests in the incubation phase as well, though this was only significant for Yellow Warblers (Fig 8C, $\chi^2 = 6.7$, $P = 0.01$). There was no indication that parasitized nests had higher failure rates during the nestling phase (Fig. 8D). While a significant portion of parasitized nests failed because natal young were out-competed by cowbirds, in both species, fewer parasitized nests failed due to nest predation, balancing overall nest losses. We found no significant differences in overall daily mortality between the species within parasitized or unparasitized nests (Fig. 8; all P's > 0.4). However, Yellow Warblers tended to have lower mortality in incubation and nestling phases for parasitized nests. Therefore, we used the mortality rates generated for each species for modeling. Unlike parasitism, daily mortality was not seasonally dependent for any of the nesting stages (program Contrast, all P's > 0.45).

Adult survival

For American Redstarts, two models fit the data reasonably well (Table 4; AICc's differed by 1.05). In the first model {Phi (.) P (g)} apparent survival was 0.39 for both sexes, but detection was much greater for males (P < 0.9) than for females (P = 0.44). The second model {Phi (T) P (g)} suggests apparent survival does not vary between sexes and is declining over time (T = trend). Again, detection for males was considerably higher (Table 4). The best model for Yellow Warblers was {Phi (g + t) P (g + t)}, which suggests that apparent survival is different between males and females, yet varies over time in a similar manner for both sexes (Table 5).

These survival rates are considerably lower than published estimates (Nichols et al. 1981), and in the case of American Redstarts, even our high 95% confidence interval for the best model (49.3%) is lower than previous estimations, which range from 50% to 70% (Nichols et al. 1981, Holmes et al 1989, Holmes and Sherry 1992). Thus we use our estimates as low estimated survival, our high 95% confidence interval as a higher estimated survival, and a high estimation of 64% for modeling purposes (Nichols et al. 1981, Hunt 1998). The high 95% confidence interval for Yellow Warblers (62%) is the same as found for Yellow Warblers previously (Nichols 1981) thus we use these the mean (40%) and the high confidence interval (Table 5) for models.

Seasonal reproductive success and population growth

Both Yellow Warblers and American Redstarts appear to be unsustainable under current levels of nest predation and brood parasitism, as even under the most optimistic projections of adult and juvenile survival, λ of both species is clearly less than 1 (Table 6). Under current levels of nest predation and brood parasitism Yellow Warblers are producing 1.5 young per female, and American Redstarts are producing only .99 young per female (Table 7). These projections are mirrored by actual declines in American Redstart nesting densities (Fig. 9A; $r^2 = 0.91$, $P = 0.018$). This decline closely matches the λ value of 0.80 obtained when we use adult survival estimates from the literature (64%) and set juvenile survival at 50% of adult survival. Yellow Warblers, by contrast, do not appear to be declining in the Bitterroot Valley (Fig. 9B; $r^2 = 0.03$, $P = 0.77$). However, even under the most optimistic estimates of adult and juvenile survival, our modeling results suggest that λ is still only 0.95 (Table 6), producing a population decline of 5% each year (Fig. 9B, dashed line). Unless adult and juvenile survivals are higher than our highest estimates for Yellow Warblers, our results suggest that this population is being sustained through immigration from other populations.

With current levels of nest predation, stable population growth for American Redstarts would only be reached if adult survival were at least 69%, even under the most optimistic juvenile survival estimates (juvenile survival = 70% of adult survival), and without any parasitism (Fig. 10). Under the same optimistic projections of juvenile survival, Yellow Warblers would need an adult survival of 56% to obtain stable population growth ($\lambda = 1$), and adult survival would need to be above 60% if we assume juvenile survival is 50% of adult survival (Fig. 10). Under current levels of parasitism, American Redstart adult survival would need to be above 72% and Yellow Warbler adult survival would need to be above 61% for stable population growth, even with juvenile survival set at 70% of adult survival for both species.

Brood parasitism, seasonal fecundity, and the importance of clutch size, fledging success, and re-nesting

The seasonal fecundity of both species was strongly affected by the rate of nest parasitism (Fig 11A), and the magnitude of the effect was similar. A 10% increase in observed parasitism caused an average decrease in seasonal fecundity of 0.09 for American Redstarts and 0.11 for Yellow Warblers. However, seasonal fecundity for American Redstarts was much lower than for Yellow Warblers overall, averaging only 1.32 fledglings per female without any parasitism, while Yellow Warblers produced 2.38 fledglings per female without parasitism (Fig. 11A, Table 7).

Differences in clutch size, fledging success and re-nesting rates all contributed to these large differences in seasonal fecundity between the species. When parasitism is low, the life-history trait that caused the largest difference in seasonal fecundity between the two species was clutch size (Fig. 11B). Without parasitism, American Redstart models run with Yellow Warbler clutch size parameters increased seasonal fecundity by 0.4 young per female, a 25% increase over the null model (run with actual values for the species). The effect of clutch size differences declined with increasing parasitism, but continued to have the largest effect throughout most of the range of parasitism (Fig 11B). Yellow Warbler models run with American Redstart clutch size showed a similar trend of larger effects when parasitism was low. The difference in fledging success had a slightly greater impact on seasonal fecundity as parasitism increased, while the reverse trend was seen for re-nesting; redstart models ran using the Yellow Warbler re-nesting values showed greater gains in seasonal fecundity when parasitism was low and Yellow Warbler models run with redstart re-nesting rates showed greater declines in seasonal fecundity when parasitism was low (Fig. 11B).

At current levels of parasitism pressure (61% observed) Yellow Warbler models run with redstart clutch size or with redstart re-nesting rates showed decreases in seasonal fecundity of an equal amount (Fig. 11B), and at higher levels of parasitism, differences in re-nesting had a greater effect than differences in clutch size.

The relative effects of brood parasitism and nest predation

Reducing daily predation rates by 10% below current rates had a greater impact on the seasonal fecundity of American Redstarts than on Yellow Warblers, and the effect was greater for both species when parasitism pressure was low (Fig. 12). The effect of reducing daily parasitism rates by 10% was dependent on the level of observed parasitism, having the largest effect when observed parasitism was between 50 and 70% for American Redstarts and between 60% and 80% for Yellow Warblers.

The relative insensitivity of Yellow Warbler seasonal fecundity to changes in predation was primarily due to their higher re-nesting rates, and their relatively constant high clutch size throughout the season. Without parasitism, 55% of redstarts stopped nesting after a single nest attempt, including 48% of pairs which failed to produce young (Fig. 13A and C). While 48% of all Yellow Warbler pairs also stopped nesting after a single nesting attempt, the vast majority of these were successful pairs, less than 25% of Yellow Warblers with failed first attempts stopped nesting (Fig. 13B and D). This increased re-nesting reduced the effect of nest failure on seasonal reproductive success. While later nests do not yield as many young due to smaller clutch size, this effect is not nearly as pronounced for Yellow Warblers as in American Redstarts (Fig 4). Thus the value of later nesting attempts is greater for Yellow Warblers, increasing the benefit of re-nesting. Indeed, more than 90% of all American Redstart fledglings come from the first 2 nesting attempts regardless of parasitism (13G), while 18% to 25% of Yellow Warbler fledglings are produced by third and fourth nesting attempts when parasitism is 50% or higher (13H).

Discussion

Our results demonstrate that under current levels of brood parasitism, the populations of both species are producing too few young to be sustainable given the apparent survival of these populations. Generalized models relating seasonal fecundity to survival of passerine birds also support these conclusions (Robinson et al. 1995b, Martin et al. 1996). The density of American Redstarts has declined at a rate closely matching expected declines from our estimations of population health, suggesting that this population is receiving little net immigration from other areas. In contrast, Yellow Warbler populations have remained stable over five years, a finding that cannot be reconciled with the demographic status of the population. These findings illustrate the pitfalls of using density as an indicator of population health (Van Horne 1983) and support the need for demographic studies.

At what level of brood parasitism do these populations balance mortality with local recruitment?

Under current levels of nest predation, even the complete removal of parasitism would not be enough to stabilize populations of American Redstarts. In the absence of parasitism, Yellow Warblers would approach a stable population only under our high projection of adult survival and with juvenile survival above 36%, (60% of adult survival). Even though parasitism exacts extremely large costs on both species, reducing seasonal fecundity by over 25% at current levels of parasitism, stable population growth would likely not be achieved unless nest predation were also reduced substantially.

Nest predation reduces seasonal fecundity wholly through reductions in nest success, but the effects of brood parasitism are more complex, causing reductions in clutch size, fledging success and nest success. Brood parasitism also affects re-nesting rates, because single-brooded females that fledge a cowbird do not re-nest, regardless of whether they fledge any natal young. The levels of natal egg removal found in these populations here are among the largest recorded (Goossen and Sealy 1982, Weatherhead 1989), and may represent an underestimated impact of cowbirds on host reproductive success, particularly for single-brooded passerines. When females produce only a single successful brood in a season, the removal of a single egg from a clutch that fledges young reduces seasonal fecundity by 25% in a four-egg clutch and 33% in a 3 egg clutch (Tewksbury et al. in prep – chapter 4). This effect, combined with the large decrease in nest success (Table 6), and the 15% - 30% decrease in fledging success from parasitized nests, suggests that most single-brooded passerines will be unable to maintain stable populations under a wide range of predation rates if parasitism rates are above 30 to 50% (Pease and Grzybowski 1995, Robinson et al. 1995b).

While seasonal fecundity appears too low to allow these populations to be successful even under optimistic survival estimations, our estimates of adult survival are also well below published estimates (Nichols et al. 1981, Holmes et al. 1989, Holmes and Sherry 1992). Our female survival values must be viewed with caution, given the low detection probabilities (Martin et al. 1995). However, survival rates for males were similarly low with high detection probabilities for both species. Sex bias in return rates, when present, typically show females with lower return rates than males (Nolan 1978, Payne and Payne 1990, Payevsky et al. 1997, Siriwardena et al. 1998, Marshall et al. 2000). Therefore, local apparent survival for females is unlikely to be higher than 60%

for either species, well below what is needed for sustainable population growth given current seasonal fecundity.

The importance of clutch size, fledging success, and re-nesting

Both species studied have small body size, are in the same subfamily, and nest in similar habitat. They are also similar in many other aspects which are commonly thought to determine the demographic impact of nest predation and brood parasitism on hosts, including timing of the breeding cycle (Robinson et al. 1995b), nest placement (Martin 1992, 1993a 1993b), and incubation time (Goldwasser et al. 1980, Grzybowski et al. 1986). However, even with these similarities, seasonal fecundity differed by 0.7 to 0.86 young per pair per season, depending on the rate of parasitism. These results suggest that models used to predict seasonal fecundity will have to incorporate the biology of the individual species in considerable detail.

Yellow Warblers are often cited as being somewhat resistant to the effects of brood parasitism due to their tendency to abandon parasitized nests and bury parasitized clutches by building a new nest on top of the old one (Clark and Robertson 1981, Burgham and Picman 1989, Sealy 1992, Robinson et al. 1995b). While these behaviors were common in our population, overall abandonment was similar between the species, and there was no difference in the building times of re-nests between the two species. Thus the burying behavior of the Yellow Warbler does not appear to confer an advantage in time savings between nesting attempts, and does not explain differences in seasonal fecundity between species. However, differences in clutch size, fledging success, and re-nesting all influenced the seasonal fecundity of these species.

Our examination of life history traits was not a traditional sensitivity analysis, where each trait is varied the same small amount while all other traits are held constant (Caswell 1989, McDonald and Caswell 1993). Instead, we were interested in the importance of each trait in contributing to the overall difference in seasonal fecundity between the two species. By switching trait values between the species, we could explicitly examine the contribution of each difference to overall seasonal fecundity.

All three life-history traits favored greater seasonal fecundity in Yellow Warblers as compared to American Redstarts, but the importance of the different traits varied across the spectrum of parasitism. Re-nesting rates and fledging success are now commonly included in models estimating seasonal fecundity (Donovan 1995, Pease and Grzybowski 1995, Woodworth 1997, 1999, Schmidt and Whelan 1999) but to date, no models have explicitly examined the effects of clutch size as the season progresses. Yellow Warblers maintain relatively large clutches throughout the season, while American Redstart clutch sizes decline sharply as the season progresses (Fig. 4). This difference in clutch size decline has the largest effect when brood parasitism is relatively infrequent because parasitism decreases nesting success and the difference in clutch size is greater in unparasitized nests.

The differences in the percent of the brood fledged was the only trait considered that became more important with increasing levels of parasitism, because the difference between these species in the percentage of the brood that fledges is much greater in parasitized nests. American Redstarts rarely fledge more than one of their own young with a cowbird nestling in the nest, while Yellow Warblers often fledge 2 or 3 natal young and a cowbird.

Our results suggest that re-nesting itself has a large effect on seasonal fecundity, as over 40% of fledglings come from second and third attempts. Increased re-nesting is always beneficial unless it affects adult survival, a possibility not explored here. The advantages of re-nesting decline slightly with increasing brood parasitism because re-nesting and clutch size differences are multiplicative in their effect on seasonal fecundity. Re-nesting will have a greater effect on seasonal fecundity when clutch size remains high later in the season. When parasitism rates are high, the value of re-nesting is reduced because the expected gain from an additional nest is low. This is intensified for the American Redstart, because in our population, parasitism increases later in the season.

Previous models incorporating re-nesting have often used a fixed number of re-nests (Donovan 1995, Schmidt and Whelan 1999). More complex models have instead fixed the breeding season length as the time between the median date when pairs begin their first nesting attempt to the median date when pairs no longer re-nest following nest failure (Pease and Grzybowski 1995), assuming all pairs re-nest if their nest fails within this period. The following method is clearly more applicable to the species studied here, as the probability of re-nesting was highly dependant on the day within the season of nest failure. To test the importance of this difference in modeling, we parameterized Schmidt and Whelan's (1999) model using their fixed re-nesting probabilities (Schmidt and Whelan 1999, equation 2), to examine the potential bias in using this approach.

Schmidt and Whalen assume that females always re-nest after a nest is predated until they have completed three attempts, at which point they stop nesting. They separate abandonment following parasitism from nest predation, and assume that females will re-nest following abandonment until they have completed four nesting attempts, at which point they stop nesting. They then vary rates of nest predation, brood parasitism, abandonment probability, and the severity of brood parasitism (defined as the difference between the number of young fledged from unparasitized nests and parasitized nests) to create seasonal fecundity isopleths as a function of different rates of nest predation and brood parasitism (Schmidt and Whelan 1999, Figs 2 and 3). The isopleths are lines along which seasonal fecundity is constant. They state that their model is presented as a tool for understanding the effects of abandonment and re-nesting, not as a means to estimate seasonal fecundity, but they use these isopleths to infer the effect of reducing nest predation or brood parasitism on seasonal fecundity. These inferences depend on the shape of the isopleths, which in turn depend on the ability of the model to correctly estimate seasonal fecundity. To parameterize their basic model, we determined the five parameters that make up their model: 1) parasitism rates (*N*, our observed parasitism), 2) nest failure rates (*P*, called predation rates in their model, but for the purpose of estimating seasonal fecundity, this is actually the percentage of nests that fail by all causes other than parasitism), 3) the mean number of young produced by successful unparasitized nests (*E*), 4) the percentage of parasitized nests that are abandoned (a_p), and 5) parasitism severity, or brood loss (*R*). *R* is calculated by determining the mean number mean number of young produced by parasitized nests (this includes nests that fail to produce any natal young but raise a cowbird successfully), and subtracting that number from the number of young produced by unparasitized nests. Using our data, for American Redstarts, $N = 0.37$, $P = 0.61$, $E = 3.33$, $a_p = 0.36$, and $R = 2.51$, while for Yellow Warblers $N = 0.61$, $P = 0.71$, $E = 3.50$, $a_p = 0.40$, and $R = 1.82$.

Using their assumptions regarding re-nesting, under current parasitism levels, American Redstarts would have a seasonal fecundity of 2.2, over double our estimate of 0.99, and Yellow Warblers would have a seasonal fecundity of 2.0, also higher than our estimate of 1.52. Because their basic model fails to account for re-nesting, and does not consider the effect of declining clutch sizes throughout the season, it dramatically overestimates seasonal fecundity, and generates higher seasonal fecundity estimates for American Redstarts than Yellow Warblers. Schmidt and Whelan (1999) readily admit that re-nesting functions may vary, and they use a fixed rate to simplify their model. However, we suggest that the shape of their seasonal fecundity isopleths may change considerably if they included more realistic assumptions regarding re-nesting rates. Future comparisons between the relative impact of nest predation and brood parasitism will require more realistic assumptions regarding re-nesting.

The relative impact of brood parasitism and nest predation

The strong curvilinear effect of decreasing daily parasitism is due to the log-linear relationship between daily parasitism and the percentage of nests that actually become parasitized. A reduction in daily parasitism of 10% creates a change in the percentage of nests parasitized of between 0.9% to 4.1%, depending on the original daily parasitism rate, as many nests which would have been parasitized on the first or second day they were available are simply parasitized later, on the fourth or fifth day of susceptibility. The effect of a daily reduction of 10% is strongest when daily rates range from 0.1 to 0.14, yielding a 60% to 70% rate of parasitism pressure. The same curvilinear relationship would apply to predation; at very high levels of nest predation, reductions in predation pressure would simply cause many nests to be predated slightly later in the nesting cycle, and would have little effect on nest success. However, since we reduced daily nest predation by 10% from a single observed daily predation rate for each species and the daily rates are similar, the result is a linear relationship across the range of parasitism. Our reduction of daily predation by 10% resulted in a 3% reduction in nest failure rates for unparasitized nests of each species). Daily rates of brood parasitism and nest predation must be raised to the power of the number of days in the period of exposure to calculate the effect on the percentage of nests parasitized and depredated; in the case of parasitism, the period is 8 days, in the case of nest predation, the period is the length of the nesting cycle, 31 days for these species. The use of daily rates, however, allows explicit comparisons of processes that act over different periods in the nesting cycle, and they allow us to compare of the probable effect of reducing cowbird numbers by 10% to the effect of reducing predator populations by 10%, because they compare change in the processes under consideration, rather than the outcome of these processes. In addition, using a daily rate of parasitism allows us to directly estimate the parameter of greatest interest – the rate at which nests become parasitized, regardless of predation rates.

A 10% decrease in daily nest predation had a greater impact on the seasonal fecundity of American Redstarts than a 10% decrease in daily parasitism over the entire range of parasitism, and at current levels of nest parasitism, the effect of decreasing predation pressure is double that of decreasing parasitism pressure. Thus predation appears to be a greater limitation on seasonal fecundity of American Redstarts than brood parasitism, primarily because redstarts re-nest less often, which increases the importance of nest success. For Yellow Warblers, the relative effect of decreasing daily predation or decreasing daily parasitism was strongly conditional on rates of nest parasitism, with parasitism playing a larger role than predation when it was above 40%. Under current conditions, with a 61% parasitism rate, brood parasitism clearly constrains population growth more than nest predation. This analysis suggests that management of Yellow Warblers should focus on reducing parasitism pressure until the observed rate of parasitism falls below 40%, at which point, greater benefit will be gained by reducing predation rates. The different conclusions drawn for these two populations stem primarily from the large difference in the effect of reducing daily predation, which are in turn directly linked to the differences in re-nesting rates between the two species. Similar to findings by Pease and Grzybowski (1995) and Schmidt and Whelan (1999), we found a small range of parasitism where decreasing predation would actually lower seasonal fecundity.

The effect of decreasing parasitism pressure by 10% has a slightly greater effect on the seasonal fecundity of Yellow Warblers than on American Redstarts when parasitism rates are high (Fig. 12), despite the fact that Yellow Warblers bury cowbird eggs (Sealy 1992) and are thought to be better adapted to parasitism due to their long history of overlap with cowbirds (Robinson et al. 1995b). This is a result of the lower nest success and re-nesting rates of American Redstarts – decreasing parasitism has a smaller effect because a greater percentage of unparasitized American Redstart nests are lost to predation and other causes (Table 7), dampening the benefit of reduced parasitism.

Conclusions

Change in populations is a function of birth, death, immigration and emigration. In the two populations studied, there appear to be differences in at least three of these variables, birth, death, and at a minimum either immigration or emigration. Our study sites are located near the western edge of the range for American Redstarts (Sauer et al. 1999), thus there may be limited opportunity for immigration from surrounding areas, while Yellow Warblers occur throughout the continental United States at much greater densities, potentially allowing much greater immigration. The different population responses of these species to demographic rates that leave both populations clearly unsustainable may suggest that at the periphery of a species' breeding range (as in the case of the American Redstart), Neotropical migrants may be more isolated from other populations, and unable to buoy unsustainable populations through immigration. In contrast, nearer the center of a species' range, declining populations may go unnoticed if immigration keeps population levels constant. Due to the complexities of these processes, identifying species at risk of population collapse due to changes on the breeding grounds will require a two-pronged approach: 1) broad ranging surveys that encompass the range of the species and the diversity of habitat conditions it breeds in so that regional declines may be detected, and 2) detailed population studies to determine the demographic effect of breeding ground processes, such as nest predation and brood parasitism, and identify life-history traits that make species more or less susceptible to these causes of reproductive failure. The first approach has received considerable attention both nationally (Sauer et al. 1999) and within Western deciduous forests where these species breed (Tewksbury et al. in press). We have taken the second approach here, demonstrating that the effects of nest predation and brood parasitism are interdependent, and conditional on re-nesting rates, seasonal changes in clutch size, and the effect of parasitism on fledging success. Under current conditions, both species would benefit from reductions in either brood parasitism or nest predation, but more gains will be achieved by reducing parasitism for Yellow Warblers, and reducing nest predation for American Redstarts, due to differences in the current predation and parasitism pressure, and differences in the life-histories of these species. Future research and management of birds on their breeding grounds will clearly benefit from detailed consideration of life history, to determine the breeding ground processes most likely to lead to unsustainable populations.

Literature Cited

Biermann, G. C., W. B. McGillivray, and K. E. Nordin. 1987. The effect of cowbird parasitism on Brewer's sparrow productivity in Alberta (Canada). Journal of Field Ornithology 58:350-354.

Braden, G. T., R. L. McKernan, and S. M. Powell. 1997. Effects of nest parasitism by the Brown-headed Cowbird on nesting success of the California Gnatcatcher. Condor 99:858-865.

Brawn, J. D. and S. K. Robinson. 1996. Source-sink population dynamics may complicate the interpretation of long-term census data. Ecology 77:3-12.

Burgham, M. C. J. and J. Picman. 1989. Effect of Brown-headed Cowbirds on the evolution of Yellow Warbler anti-parasite strategies. Animal Behavior 38:298-308.

Burnham, K. P. and D. R. Anderson. 1998. Model selection and inference: A Practical Information Theoretic Approach. Springer-Verlag, New York.

Caswell, H. 1989. Matrix population models. Sinauer Associates, Inc., Sunderland, MA.

Clark, K. L. and R. J. Robertson. 1981. Cowbird (*Molothrus ater*) parasitism and evolution of antiparasite strategies in the Yellow Warbler (*Dendroica petechia*). Wilson Bulletin 93:249-258.

Donovan, T. M., P. W. Jones, E. M. Annand, and F. R. Thompson III. 1997. Variation in local-scale edge effects: mechanisms and landscape context. Ecology 78:2064-2075.

Donovan, T. M., R. H. Lamberson, A. Kimber, F. R. Thompson III, and J. Faaborg.

1995. Modeling the effects of habitat fragmentation on source and sink demography of neotropical migrant birds. Conservation Biology 9:1396-1407.

Goldwasser, S., D. Gaines, and S. R. Wilbur. 1980. The Least Bell's Vireo in California: a de facto endangered race. American Birds 34:742-745.

Goossen, J. P. and S. G. Sealy. 1982. Production of young in a dense nesting population of Yellow Warblers, Dendroica petechia, in Manitoba (Canada). Canadian Field-Naturalist 96:189-199.

Greenberg, R. 1980. Demographic aspects of long-distance migration. Pages 493-505 *in* A. Keast and E. S. Morton, eds. Migrant birds in the Neotropics: ecology, behavior, distribution, and conservation. Smithsonian Institute Press, Washington DC.

Grzybowski, J. A., R. B. Clapp, and J. T. Jr. Marshall. 1986. History and current population status of the Black-headed Vireo in Oklahoma. American Birds 40:1151-1161.

Hagan, J. M., III and D. W. Johnson. 1992. Ecology and conservation of Neotropical migrant landbirds. Smithsonian Institute Press, Washington D.C.

Hensler, G. L. and J. D. Nichols. 1981. The Mayfield method of estimating nesting success: a model, estimators and simulation results. Wilson Bulletin 93:42-53.

High Performance Systems Inc. 1998. Stella Research Software 5.11. High Performance Systems, Inc., Hanover, NH.

Holmes, R. T. and T. W. Sherry. 1992. Site fidelity of migratory warblers in temperate breeding and Neotropical wintering areas: implications for population dynamics, habitat selection, and conservation. *in* J. M. Hagan, III and D. W. Johnston, eds. Ecology and conservation of Neotropical migrant landbirds. Smithsonian Institute Press, Washington DC.

Holmes, R. T., T. W. Sherry, and L. Reitsma. Population structure, territoriality and overwinter survival of two migrant warbler species in Jamaica. Condor 91[3], 545-561. 1989.

Hunt, P. D. Evidence from a landscape population model of the importance of early successional habitat to the American Redstart. Conservation Biology 12[6], 1377-1389. 1998.

Jehl, J. R. and N. K. Johnson. 1994. A century of avifaunal change in western North American. Studies in Avian Biology No, 15, Cooper Ornithological Society.

King, J. R. and L. R. Mewaldt. 1987. The summer biology of an unstable insular population of White-crowned Sparrows in Oregon. Condor 89:549-565.

Kus, B. E. 1999. Impacts of Brown-headed Cowbird parasitism on the endangered Least Bell's Vireo. Studies in Avian Biology 18:160-166.

Marra, P. P., K. A. Hobson, and R. T. Holmes. 1998. Linking winter and summer events in a migratory bird by using stable-carbon isotopes. Science 282:1884-1886.

Martin, T. E. 1992. Breeding productivity considerations: what are the appropriate habitat features for management. *in* J. M. Hagan, III and D. W. Johnston, eds. Ecology and conservation of Neotropical migrant landbirds. . Smithsonian Institution Press, Washington D.C.

Martin, T. E. 1993. Nest predation among vegetation layers and habitat types: revising the dogmas. American Naturalist 141:897-913.

Martin, T. E. 1993. Nest predation and nest sites: new perspectives on old patterns. Bioscience 43:523-532.

Martin, T. E., I. J. Ball, and J. Tewksbury. 1996. Environmental perturbations and rates of nest predation in birds. Transactions Of The North American Wildlife And Natural Resources Conference 61:43-49.

Martin, T. E., J. Clobert, and D. R. Anderson. 1995. Return rates in studies of life history evolution: are biases large? Journal of Applied Statistics 22:863-875.

Martin, T. E. and D. M. Finch. Ecology and management of Neotropical migratory birds; a synthesis and review of critical issues. Oxford University Press, New York.

Martin, T. E., W. Hochachka, C. J. Conway, and W. J. Jenkins. 1996. BBIRD field protocol. Montana Cooperative Wildlife Research Unit, University of Montana, Missoula, MT.

Mayfield, H. F. 1961. Cowbird parasitism and the population of the Kirkland's Warbler. Evolution 15:174-179.

Mayfield, H. F. 1961. Nesting success calculated from exposure. Wilson Bulletin 73:255-261.

Mayfield, H. F. 1975. Suggestions for calculating nest success. Wilson Bulletin 87:456-466.

McDonald, D. B. and H. Caswell. 1993. Matrix methods for avian demography. Current Ornithology 10:139-185.

Newton, I. 1998. Population limitation in birds. Academic Press, San Diego, CA.

Nichols, J. D., B. R. Noon, S. L. Stokes, and J. E. Hines. 1981. Remarks on the use of mark-recapture methodology in estimating avian population size. Studies in Avian Biology 6:121-136.

Nolan, V. Jr. 1978. The ecology and behavior of the Prairie Warbler *Dendroica discolor*. Ornithological Monographs No. 26. American Ornithologists Union, Washington, DC.

Payevsky, V. A., V. G. Vysotsky, V. D. Yefremov, M. Y. Markovets, Y. G. Morozov, and A. P. Shapoval. 1997. Sex-specific survival rates in birds. Zhurnal-Obshchei-Biologii 58:5-20.

Payne, R. B. and L. L. Payne. 1990. Survival estimates of indigo buntings: comparison of banding recoveries and local observations. Condor 92:938-946.

Pease, C. M. and J. A. Grzybowski. 1995. Assessing the consequences of brood parasitism and nest predation on seasonal fecundity in passerine birds. Auk 112:343-363.

Post, W. and J. W. Wiley. 1977. Reproductive interactions of the Shiny Cowbird and the Yellow-shouldered Blackbird. Condor 79:176-184.

Rappole, J. H. and M. V. McDonald. 1994. Cause and effect in population declines of migratory birds. Auk 111:652-660.

Ricklefs, R. E. 1973. Fecundity, mortality, and avian demography. Pages 366-435 *in* D. S. Farner, ed. Breeding biology of birds. National Academy of Sciences, Washington DC.

Robbins, C. S., J. R. Sauer, R. Greenberg, and S. Droege. 1989. Population declines in North American birds that migrate to the Neotropics. Proc. Natl. Acad. Sci. 86:7658-7662.

Robinson, S. K., S. I. Rothstein, M. C. Brittingham, L. J. Petit, and J. A. Grzybowski. 1995. Ecology and behavior of cowbirds and their impact on host populations. Pages 428-460 *in* T. E. Martin and D. M. Finch, eds. Ecology and management of neotropical migratory birds: a synthesis and review of critical issues. Oxford University Press, New York.

Robinson, S. K., F. R. Thompson III, T. M. Donovan, D. R. Whitehead, and J. Faaborg. 1995. Regional forest fragmentation and the nesting success of migratory birds. Science 267:1987-1990.

Rogers, C. M., M. J. Taitt, J. N. M. Smith, and G. Jongejan. 1997. Nest predation and cowbird parasitism create a demographic sink in wetland-breeding song sparrows. Condor 99:622-633.

Sauer, J. R., J. E. Hines, G. Gough, I. Thomas, and B. G. Peterjohn. 1999. The North American breeding bird survey results and analysis 1966-1998. Version 98.1. Patuxent Wildlife Research Center, Laurel, MD.

Sauer, J. R. and B. K. Williams. 1989. Generalized procedures for testing hypotheses about survival and recovery rates. Journal of Wildlife Management 53:137-142.

Schmidt, K. A. and C. J. Whelan. 1999. The relative impacts of nest predation and brood parasitism on seasonal reproductive success. Conservation Biology 13:46-57.

Sealy, S. G. 1995. Burial of cowbird eggs by parasitized Yellow Warblers: an empirical and experimental study. Animal Behavior 49:877-889.

Sealy, S. G. 1992. Removal of Yellow Warbler eggs in association with cowbird parasitism. Condor 94:40-54.

Sherry, T. W. and R. T. Holmes. 1996. Winter habitat quality, population limitation, and conservation of Neotropical-Nearctic migrant birds. Ecology 77:36-48.

Siriwardena, G. M., S. R. Baillie, and J. D. Wilson. Variation in the survival rates of some British passerines with respect to their population trends on farmland. Bird-Study 45[3], 276-292. 1998.

Temple, S. A. and J. R. Cary. 1988. Modeling dynamics of habitat-interior bird populations in fragmented landscapes. Conservation Biology 2:340-347.

Terborgh, J. W. Where have all the birds gone? Princeton University Press, Princeton, NJ.

Tewksbury, J. J., A. E. Black, N. Nur, G. R. Guepel, V. A. Saab, B. D. Logan, and D. S. Dobkin. in press. Effects of anthropogenic fragmentation and livestock grazing on western riparian bird communities. Studies in Avian Biology.

Tewksbury, J. J., S. J. Hejl, and T. E. Martin. 1998. Habitat fragmentation in a Western landscape: breeding productivity does not decline with increasing fragmentation. Ecology 79:2890-2903.

Trail, P. W. and L. F. Baptista. 1993. The impact of Brown-headed Cowbird parasitism on populations of the Nuttall's White-Crowned Sparrow. Conservation Biology 7:309-315.

Van Horne, B. 1983. Density as a misleading indicator of habitat quality. Journal of Wildlife Management 47:893-901.

Weatherhead, P. J. 1989. Sex ratios, host-specific reproductive success, and impact of Brown-headed Cowbirds. Auk 106:358-366.

White, G. C. and K. P. Burnham. 1999. Program MARK: Survival estimation from populations of marked animals. Bird Study 46 Supplement:120-138.

Woodworth, B. L. 1997. Brood parasitism, nest predation, and season-long reproductive success of a tropical island endemic. Condor 99:605-621.

Woodworth, B. L. 1999. Modeling population dynamics of a songbird exposed to parasitism and predation and evaluating management options. Conservation Biology 13:67-76.

Table 1: Parameters used to build the seasonal fecundity model

	Description	American Redstart	Yellow Warbler
Id	Nesting initiation distribution in season days (*Sd*)	normal distribution (SD 3.7 days)	normal distribution (SD 4.7 days)
P_P	Fraction of nests parasitized	seasonally dependent	constant
Cs	Clutch size	seasonally dependent	seasonally dependent
T_B	Building time	dependent on attempt number	dependent on attempt number
T_E	Time in egg-laying (*Cs* – 1 day)¶		
T_I	Incubation period length	11.76 days (SE = 0.1, N = 41)	10.91 days (SE = 0.04, N = 268)
T_N	Nestling period length	9.82 days (SE = 0.17, N = 39)	10.05 days (SE = 0.06, N = 220)
ds	Daily survival for building (ds_B), egg laying (ds_E), incubation (ds_I), and nestling (ds_N) periods.	dependent on parasitism (Fig. 3)	dependent on parasitism (Fig. 3)
P_F	Fledging success: percent of clutch that fledges	dependent on parasitism	dependent on clutch size and parasitism

Table 1 (cont.)

P_{RN}	Probability of re-nesting after nest failure	dependent on day in season	dependent on day in season
Sd	Day in season – for time dependent processes		

¶ The egg-laying period is one day shorter than the clutch size, as incubation generally starts the day the last egg is laid.

Table 2: Marginal means for building time as a function of attempt number from 54 nests in which the first day of building and the day of clutch initiation were known.

Attempt #	Mean (days)	se
1	7.34	0.56
2	4.69	0.68
3	4.49	0.92
4	3.06	2.20
5	3.06¶	2.20¶

¶ Building time for 5th attempts were assumed to be the same as 4th attempts, as empirical estimation was not possible.

Table 3: Logistic regression results for re-nesting, separated by species, for the predicted model, including only the season day of nest failure of the previous nest, and the full model, including season day of previous nest failure, clutch size of the previous nest, nest attempt number, and parasitism of the previous nest.

	B[‡]	*SE*	*Exp(B)*[‡]	*P*
American Redstart				
Predicted model $\chi^2 = 35$, $P < 0.001$[¶]				
season day of last nest failure	-0.123	0.025	0.884	< 0.001
constant	2.148	0.477		< 0.001
Full model $\chi^2 = 42$, $P < 0.001$[¶]				
season day of last nest failure	-0.301	0.069	0.740	< 0.001
nest attempt number	1.380	0.785	3.974	0.079
clutch size	-0.021	0.535	0.979	0.969
parasitism	-0.394	1.010	0.675	0.697
constant	3.308	2.832		0.243
Yellow Warbler				
Predicted model $\chi^2 = 35$, $P < 0.001$[¶]				
season day of last nest failure	-0.201	0.020	0.810	< 0.000
constant	5.113	0.479		< 0.000

Table 3 (cont.)

Full model $\chi^2 = 133$, $P < 0.001$[¶]				
season day of last nest failure	-0.272	0.045	0.762	< 0.001
nest attempt number	0.279	0.304	1.322	0.359
clutch size	-0.441	0.291	0.643	0.129
parasitism	0.321	0.528	1.379	0.543
constant	6.509	1.590		< 0.001

[¶] the model χ^2 is a measure of the difference between the likelihood of obtaining the observed results under the null model (constant only) and the observed model

[¥] *B* is the regression coefficient, representing the change in log odds of re-nesting with a one unit change in the independent variable, *Exp(B)* is the change in actual odds of re-nesting with a one unit change in the independent variable. Odds less than one indicate re-nesting becomes progressively less likely to occur with increases in the dependent variable, odds greater than one indicate that re-nesting is more likely to occur with a one-unit increase in the variable.

Table 4: Apparent survival estimates from best approximating models, American Redstarts

American Redstarts - best model {Phi$^{\phi}$ (.) P (g)} - AICc =207.52, Delta AICc = 0

			Apparent Survival					Detection		
Sex	year	n†	Phi$^{\phi}$	se	u-95% CI	sex	year	P	se	u-95% CI
both sexes	all years	111	0.393	0.050	0.493	males	all years	0.906	0.087	0.986
						females	all years	0.439	0.132	0.691

American Redstarts - second best model {Phi (T) P (g)} - AICc =208.57, Delta AICc = 1.05

Sex	year	n†	Phi$^{\phi}$	se	u-95% CI	sex	year	P	se	u-95% CI
Males	95-96	32	0.448	0.076	0.598	males	all years	0.902	0.090	0.985
	96-97	16	0.400	0.051	0.502	females	all years	0.438	0.131	0.689
	97-98	7	0.353	0.061	0.479					
	98-99	5	0.309	0.089	0.503					
Females	95-96	22	0.448	0.076	0.598					

Table 4 (cont.)

96-97	15	0.400	0.051	0.502
97-98	9	0.353	0.061	0.479
98-99	5	0.309	0.089	0.503

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† number of birds banded in previous year. For American Redstarts, that includes all birds banded, as survival and detection did not vary across years. For Yellow Warblers after the first year of returns, returning birds may include birds banded before the previous year, but each n is only birds banded in the previous year.

♦ Apparent survival

Detection probability

Table 5: Apparent survival estimates from best approximating model, Yellow Warblers

Yellow Warblers - best model {Phi$^{\phi}$ (g + t) P (g + t)} - AICc =1058, Delta AICc = 0

Sex	year	n[†]	Phi$^{\phi}$	se	u-95% CI	sex	year	P	se	u-95% CI
Males	95-96	158	0.562	0.061	0.676	males	95-96	0.741	0.069	0.853
	96-97	105	0.525	0.060	0.639		96-97	0.733	0.073	0.851
	97-98	48	0.413	0.054	0.521		97-98	0.805	0.070	0.908
	98-99a[¶]	64	0.468	0.045	0.557		98-99a	0.971	0.018	0.991
	99b[¥]		0.946	0.027	0.980		98-99b	1	0	1
Females	95-96	97	0.485	0.071	0.622	females	95-96	0.480	0.108	0.683
	96-97	46	0.447	0.069	0.583		96-97	0.469	0.106	0.671
	97-98	38	0.340	0.057	0.459		97-98	0.571	0.110	0.762
	98-99a[¶]	46	0.392	0.048	0.489		98-99	0.914	0.049	0.973
	99b[¥]		1	0	1		98-99b	1	0	1

Table 5 (cont.)

[†] number of birds banded in previous year. For American Redstarts, that includes all birds banded, as survival and detection did not vary across years. For Yellow Warblers after the first year of returns, returning birds may include birds banded before the previous year, but each n is only birds banded in the previous year.

[♦] Apparent survival

Detection probability

[¶] Parameters for the first half of the season (see methods)

[¥] Parameters for the second half of the season – detection probability is fixed (see methods)

Table 6: Estimated population growth (λ) without parasitism, and at observed levels of parasitism for American Redstarts and Yellow Warblers under the local estimated female survival (local) treated as a minimum estimate (see methods) the high 95% CI of our local estimate (High 95% CI) and for American Redstarts, an average published estimate, setting juvenile survival at 40%, 50%, 60% and 70% of adult survival. Value in bold most closely matches the decline in redstart density (Fig. 9). No values of λ are high enough to match line for Yellow Warblers (Fig. 9).

American Redstart no parasitism				
$S_a^{¥}$	$S_j^{¶} = 40\% S_a^{¥}$	$S_j = 50\% S_a^{¥}$	$S_j = 60\% S_a^{¥}$	$S_j = 70\% S_a^{¥}$
Local (39.3%)	0.50	0.52	0.55	0.57
Local high CI (49.3%)	0.62	0.66	0.69	0.72
Published (64%)	0.81	0.85	0.89	0.94
American Redstart observed (33%) parasitism				
Local (39.3%)	0.47	0.49	0.51	0.53
Local high CI (49.3%)	0.59	0.62	0.64	0.66
Published (64%)	0.77	**0.80**	0.83	0.86

Table 6 (cont.)

Yellow Warblers no parasitism				
Local (40%)	0.57	0.62	0.66	0.71
Local High CI (62%)	0.89	0.96	1.03	1.09
Yellow Warblers observed (61%) parasitism				
Local (40%)	0.52	0.55	0.58	0.61
Local High CI (62%)	0.81	0.86	0.90	0.95

[¥] Adult survival

[¶] Juvenile survival

Table 7: Nest success, the number fledged per successful nest (standard errors in parentheses), the average number of young fledged per nesting attempt, and seasonal fecundity (the number of young produced per females per season) for unparasitized and parasitized American Redstarts and Yellow Warblers, and the population averages under current levels of brood parasitism for each species.

	American Redstart				Yellow Warbler			
	nest success[¥]	fledged per suc. nest	fledged per nest[¶]	seasonal fecundity	nest success[¥]	fledged per suc. nest	fledged per nest[¶]	seasonal fecundity
Unparasitized nests	31.06% (4.56%)	3.31 (0.20)	1.03	1.32	35.38% (3.50%)	3.26 (0.19)	1.16	2.18
Parasitized nests	10.48% (2.81%)	1.44 (0.18)	0.15	0.39	11.98% (1.63%)	2.04 (0.18)	0.24	1.08
Entire population	22.70% (3.19%)	2.90 (0.20)	0.66	0.99	19.12% (1.31%)	2.72 (0.16)	0.52	1.52

Table 7 (cont.)

Parasitized reduction[§]	66.25%	56.39%	85.28%	70.41%	66.15%	37.60%	78.88%	50.46%
Population reduction[ι]	26.91%	12.38%	35.96%	24.72%	45.97%	16.64%	54.96%	30.17%

[¥] Mayfield adjusted percent of successful nests

[¶] the number of young fledged per nesting attempt (the product of nest success and the number fledged per successful attempt)

[§] the percent reduction in each parameter when parasitized nests are compared to unparasitized nests

[ι] the percent reduction in each parameter caused by current levels of parasitism

Figure Legends

Fig. 1: Basic construction of the demographic model used to estimate seasonal fecundity. (A) Initiation of first breeding (*Id*) through the termination of the first nesting attempt. Nests that fail may re-nest (A: P_{RN}), nests that are successful fledge young (A: *fledge_1*), as a percentage of the initial clutch size (A:P_F, see table 1). (B) detail of the nesting cycle, where daily survival rates (ds_B through ds_N) are raised to the power of the number of days in the building (*T_B*) egg-laying (*T_E*) incubation (*T_I*) and nestling (*T_N*) periods, to determine the probability of a nest failing in each period. (C) Females that re-nest (A:P_{RN}) begin a second nesting attempt and continue nesting until no females re-nest. Many parameters are seasonally dependant (see Results) thus the model tracks the timing of each event in season days (*Sd*).

Fig. 2: The two stage life-cycle diagram for female birds illustrating the matrix model used to calculate population growth. The model assumes a post-breeding census (Mcdonald and Caswell 1989). Juvenile birds survive to become adults at P_1 and adult birds have an annual survival of P_2. The fecundity transitions for first year birds and adults are F_1 and F_2, which are assumed to be equal in our model (see methods). First year fecundity is derived from the fact that these birds begin as juveniles at the end of the first breeding season, and within a year have produced young of their own, providing they survive.

Fig. 3: Timing of parasitism within the nest cycle. Day 0 is the day the first natal egg is laid (clutch initiation); incubation generally starts on the day the last egg is laid, days 2 through 5, depending on clutch size. (A) Percentage of all cowbird eggs laid in nests of both species on each day of the nest cycle. The distribution did not differ by species (F = 1.4, df 1, 296, P = 0.234). (B) As in (A), but including only those cowbird eggs laid which subsequently hatched. This distribution also did not differ by species (F = 0, df 1, 82, P = 1).

Fig. 4: Clutch Size for unparasitized (gray) and parasitized (black) American Redstarts (A) and Yellow Warblers (B) as a function of the day in the season the nest was initiated.

Fig. 5: The percent of the natal clutch size that fledges from unparasitized nests (gray) and parasitized nests (black) as a function of natal clutch size, for American Redstarts (A) and Yellow Warblers (B). Error bars are 1 standard error; sample sizes are shown in parentheses for unparasitized and parasitized nests, respectively.

Fig. 6: Re-nesting functions for (A) American Redstarts and (B) Yellow Warblers, as a function of day within the breeding season that the previous nest failed. The re-nesting probability curves are predicted values from logistic regression with the failure day of the previous nesting attempt as a predictor variable. Bars indicate

the number of cases where females either did re-nest (re-nest) or did not re-nest (no re-nest) following nest failure, as a function of season day. Dashed lines indicate the day in which 50% of the females stop re-nesting after nest failure.

Fig. 7: (A) Difference between observed parasitism (white bars) and parasitism pressure (hatched bars) for American Redstarts and Yellow Warblers. Parasitism pressure is greater than observed parasitism for both species. (B) Parasitism pressure throughout the season for American Redstarts (gray triangles) and Yellow Warblers (black circles). Season day 0 is the mean day of initiation of first attempts. Error bars are 1 standard error; the regression line is for American Redstarts, Yellow Warblers showed no significant change in parasitism pressure throughout the season.

Fig. 8: Daily mortality rates (the chance that a nest will fail over a given 24-hour period) for building, egg-laying, incubation, and nestling phases of the nest cycle for American Redstarts (open bars) and Yellow Warblers (hatched bars) for parasitized and unparasitized nests. The light gray area in each bar is mortality attributable to brood parasitism, the dark gray area is nest mortality attributable to nest predation. Error bars are for total daily mortality rates. Letters above data indicate significant differences in total daily mortality ($P <$

0.05). All tests were χ^2 tests using program Contrast. A total of 126 American Redstart nests and 423 Yellow Warbler nests are included in this analysis.

Fig. 9: The number of territories with breeding females from 1995 through 1999. American Redstarts (A) and Yellow Warblers (B). Solid lines are linear trends in density, dashed lines are predicted changes in population size (predicted λ) using the closest fitting parameters for adult and juvenile survival (Table 6) under current levels of nest predation and brood parasitism.

Fig. 10: Stable population isoclines ($\lambda = 1$) for American Redstarts (gray) and Yellow Warblers (black) as a function of adult survival and parasitism rate, under four different ratios of juvenile to adult survival.

Fig. 11: Seasonal fecundity of American Redstarts (solid line) and Yellow Warblers (dashed line) as a function of the percent of nests that are parasitized (A), and change in seasonal fecundity for American Redstarts (gray triangles) and Yellow Warblers (black circles) due to differences in clutch size, fledging success, and re-nest functions between the two species.

Fig. 12: Change in seasonal fecundity realized by a 10% drop in daily nest predation (triangles) and daily parasitism pressure (circles) for American Redstarts (gray)

and Yellow Warblers (black) across the full range of observed parasitism possible.

Fig. 13: Percentage of all females (A and B), females that stopped nesting without a successful nest (C and D) and females who's last nest was successful (E and F) for American Redstarts (left hand panels) and Yellow Warblers (right hand panels), as functions of the number of nests attempted in the season. Below (G and H), the percentage of all young fledged from 1st, 2nd, 3rd, 4th, and 5th nesting attempts for both species. All graphs show model results with parasitism set at 0% (white symbols), 50% (gray symbols) and 100% (black symbols).

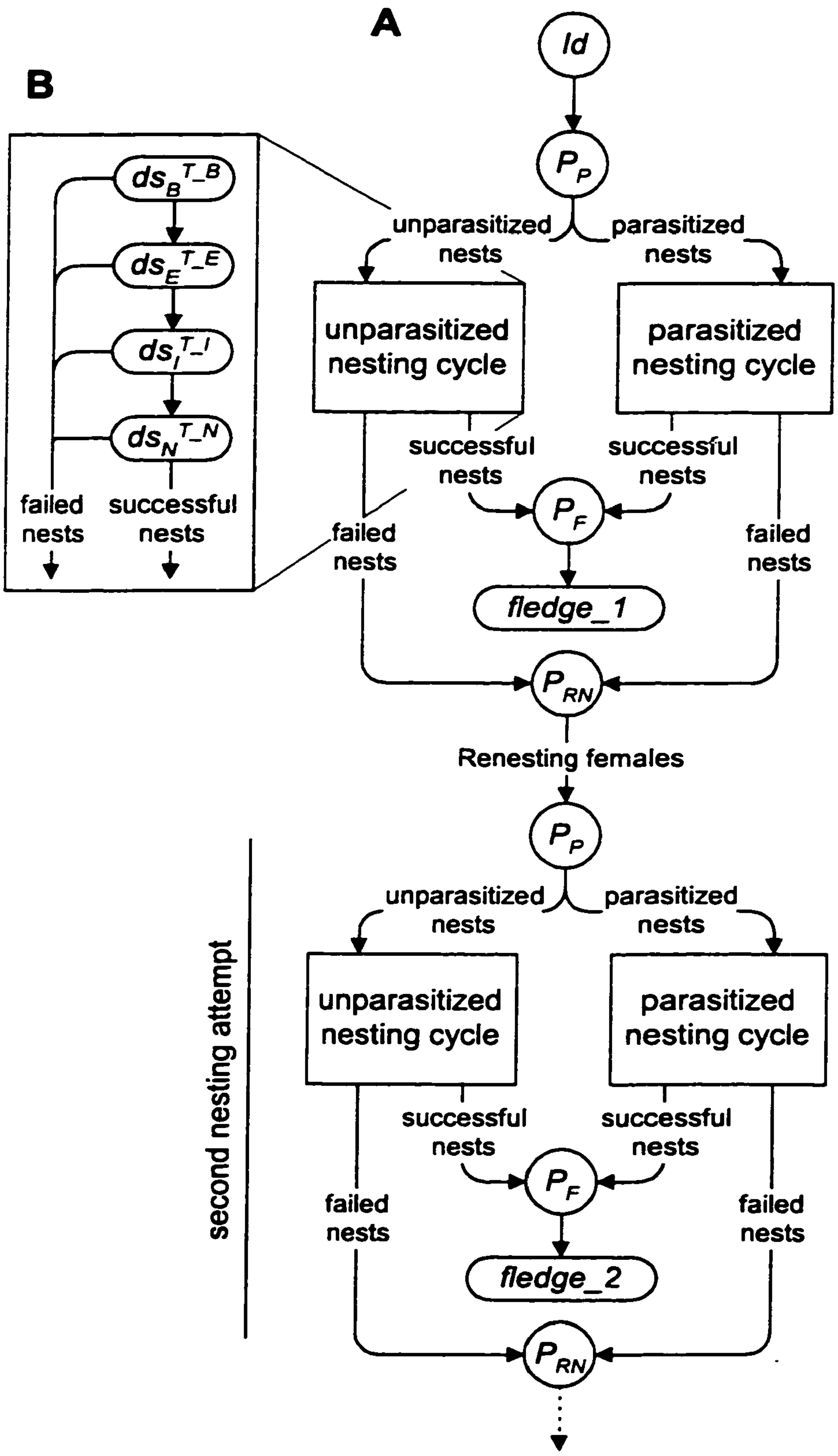

A
B
Id
P_P
unparasitized nests
parasitized nests
unparasitized nesting cycle
parasitized nesting cycle
successful nests
successful nests
P_F
failed nests
failed nests
fledge_1
P_{RN}
Renesting females
P_P
unparasitized nests
parasitized nests
unparasitized nesting cycle
parasitized nesting cycle
successful nests
successful nests
P_F
failed nests
failed nests
fledge_2
P_{RN}
second nesting attempt
$ds_B^{T\_B}$
$ds_E^{T\_E}$
$ds_I^{T\_I}$
$ds_N^{T\_N}$
failed nests
successful nests

Figure 1

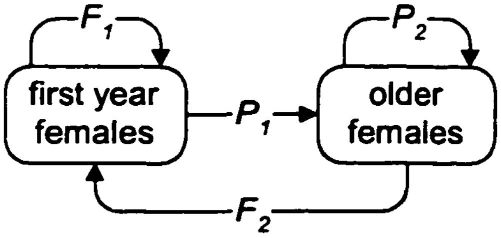


Figure 2

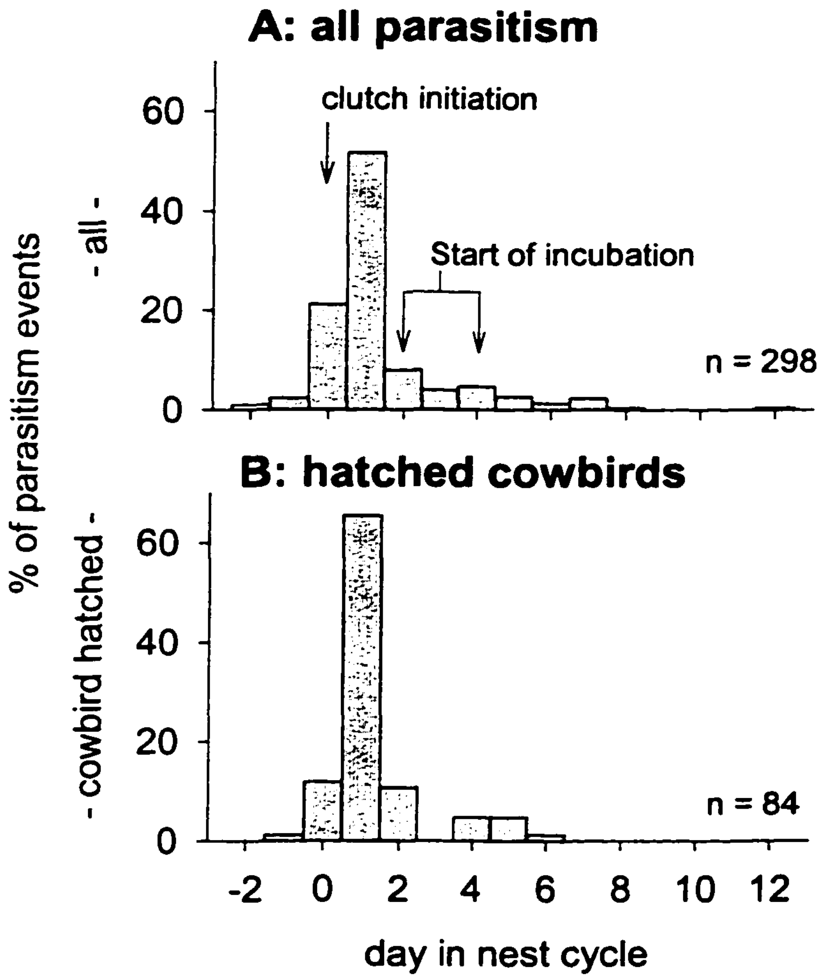

A: all parasitism
clutch initiation
Start of incubation
n = 298
B: hatched cowbirds
n = 84
% of parasitism events
- all -
- cowbird hatched -
0
20
40
60
-2
0
2
4
6
8
10
12
day in nest cycle

Figure 3

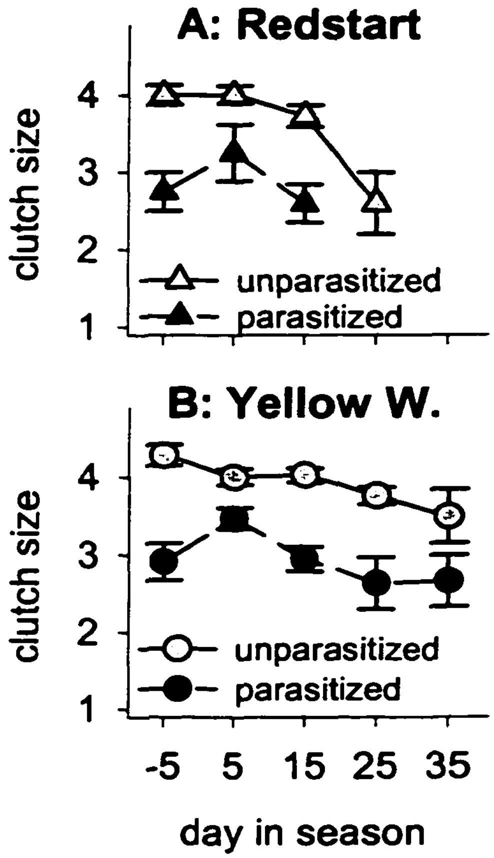

A: Redstart
clutch size
4
3
2
1
unparasitized
parasitized
B: Yellow W.
clutch size
4
3
2
1
unparasitized
parasitized
-5
5
15
25
35
day in season

Figure 4

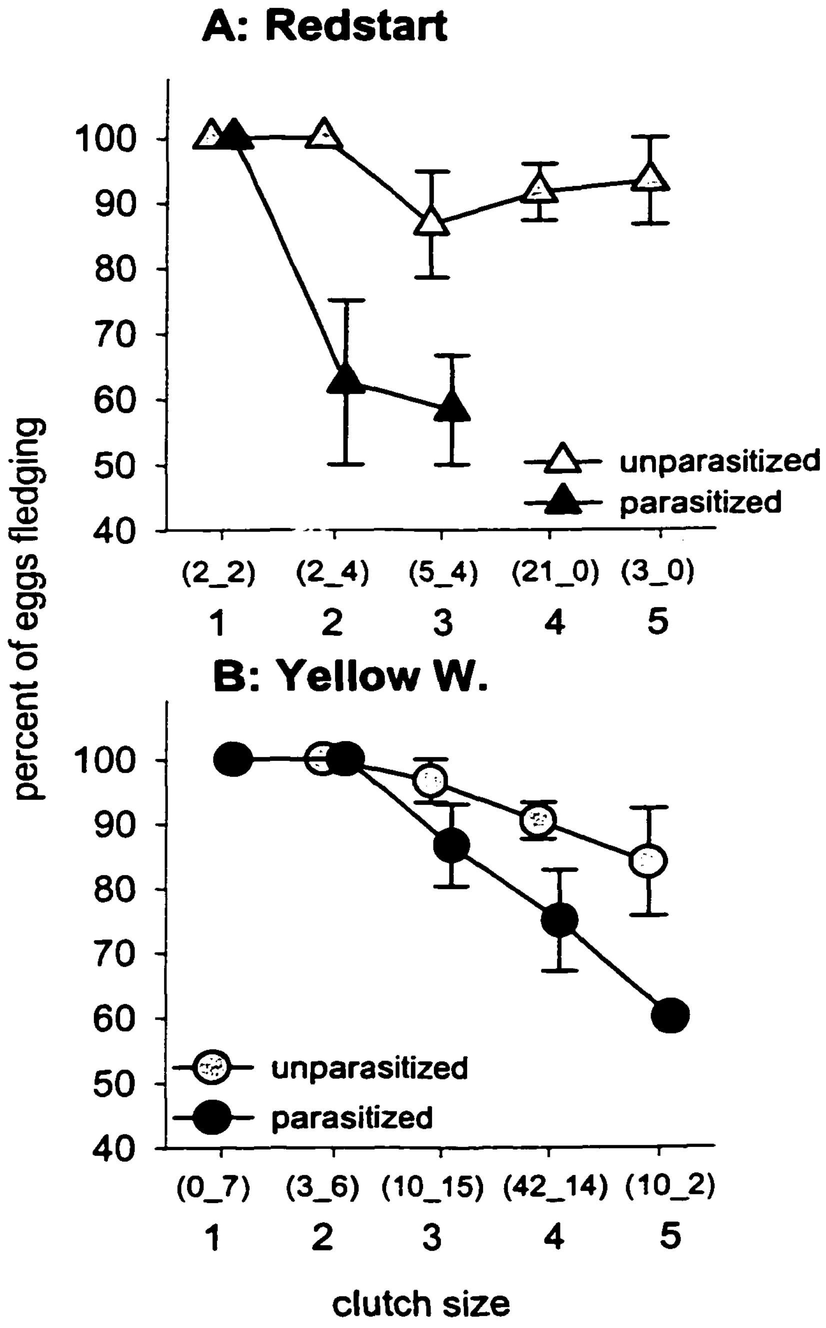
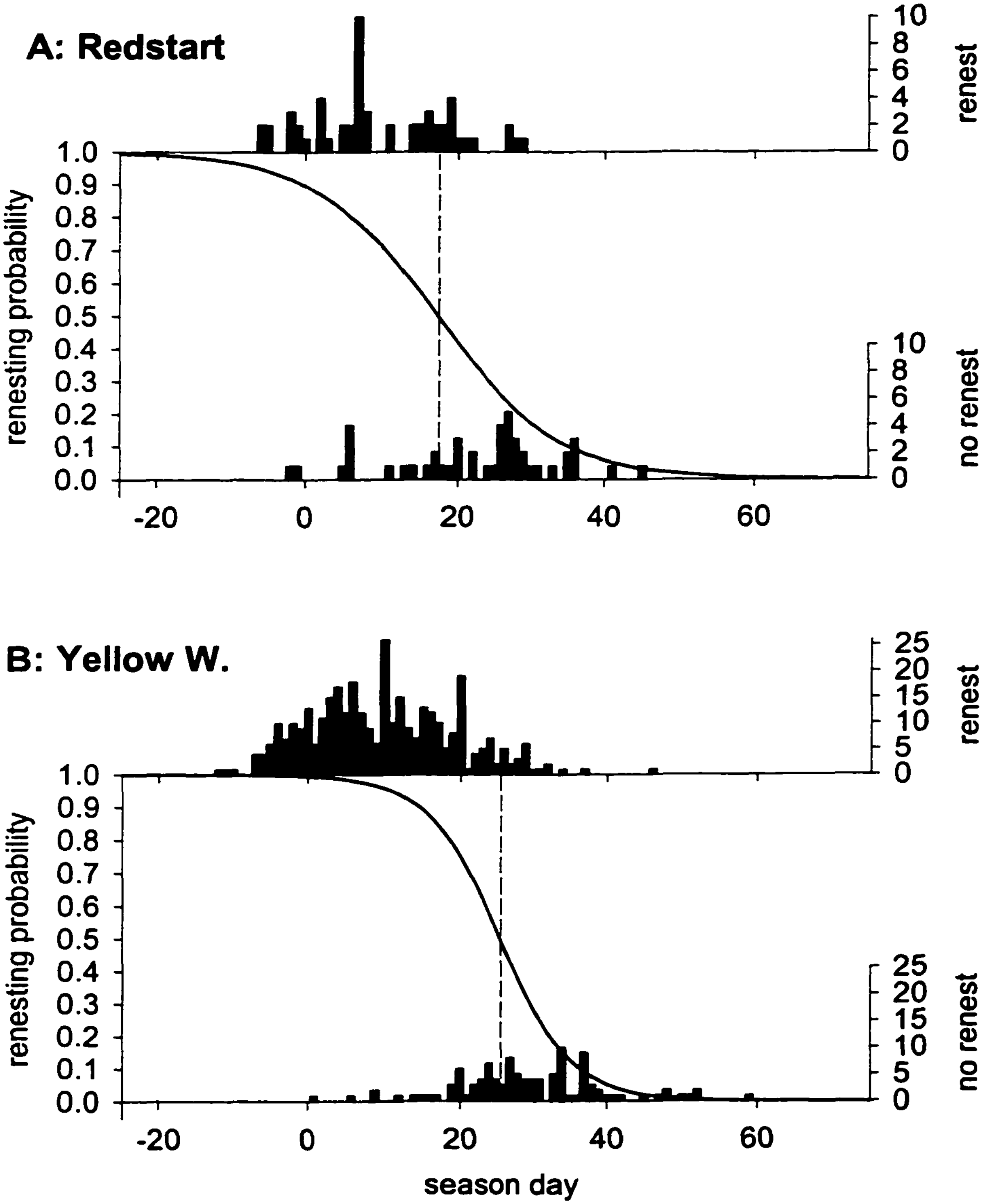

A: Redstart
100
90
80
70
60
50
40
percent of eggs fledging
unparasitized
parasitized
(2_2)
(2_4)
(5_4)
(21_0)
(3_0)
1
2
3
4
5
B: Yellow W.
100
90
80
70
60
50
40
unparasitized
parasitized
(0_7)
(3_6)
(10_15)
(42_14)
(10_2)
1
2
3
4
5
clutch size

Figure 5

Figure 6


A: Redstart
renesting probability
1.0
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0.0
-20
0
20
40
60
renest
10
8
6
4
2
0
no renest
10
8
6
4
2
0
B: Yellow W.
renesting probability
1.0
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0.0
-20
0
20
40
60
season day
renest
25
20
15
10
5
0
no renest
25
20
15
10
5
0

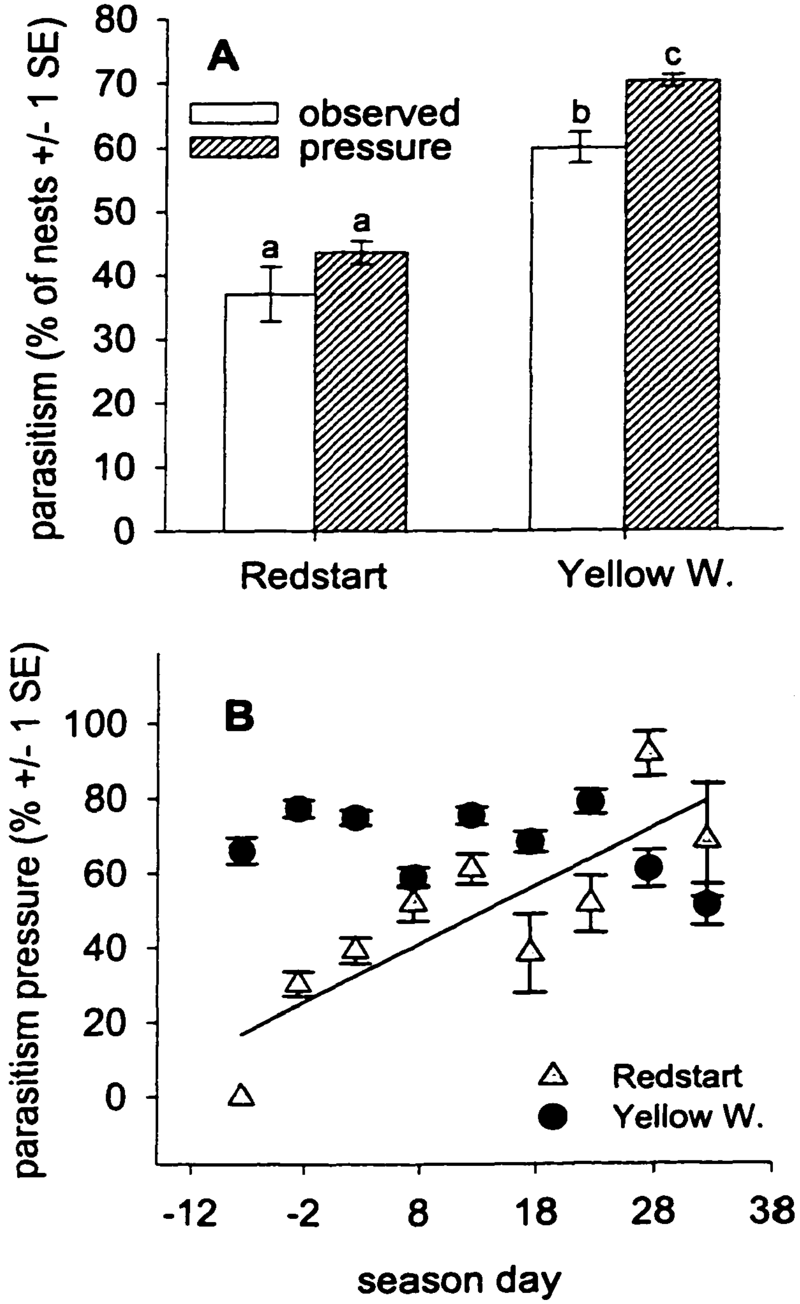
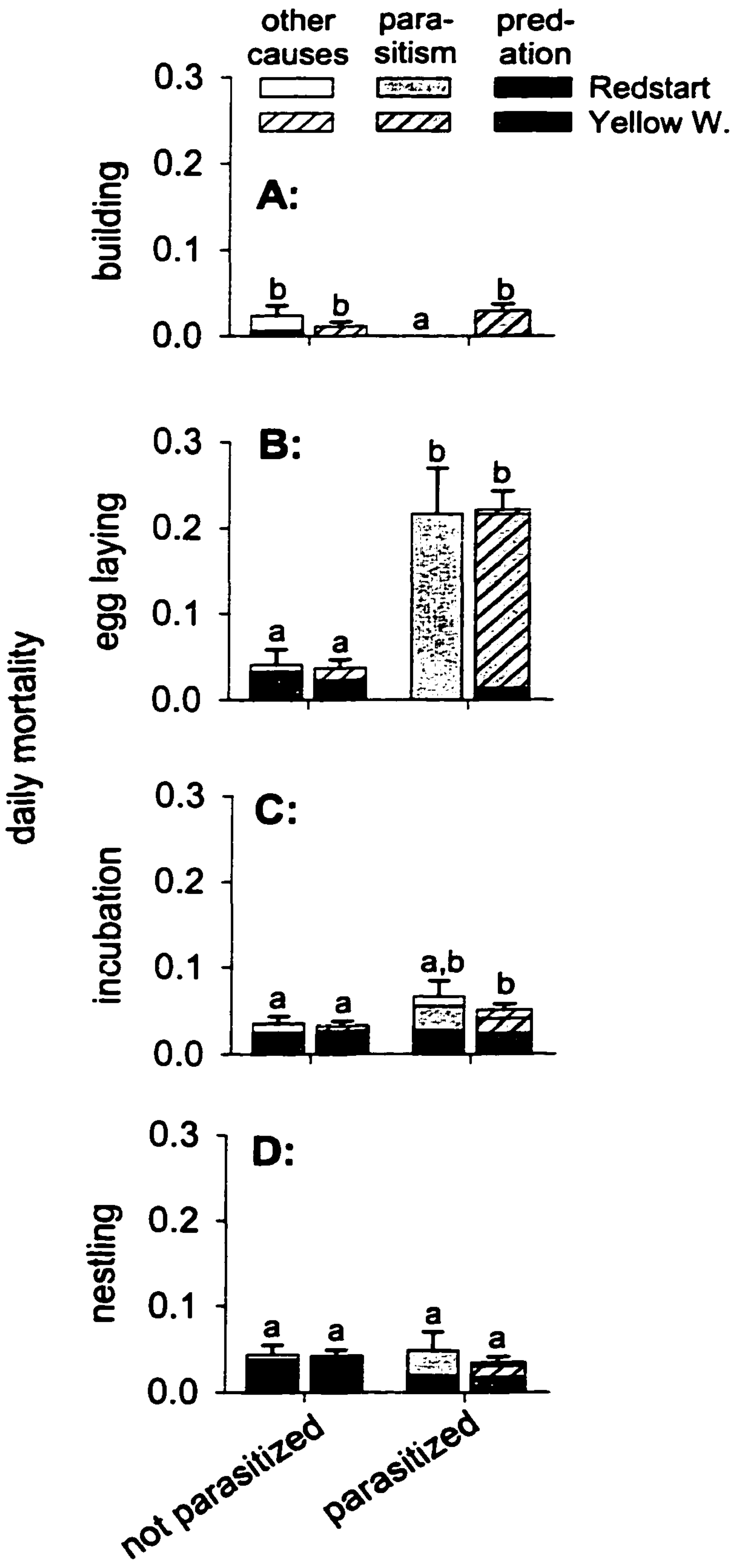

A
observed
pressure
parasitism (% of nests +/- 1 SE)
0
10
20
30
40
50
60
70
80
a
a
b
c
Redstart
Yellow W.
B
parasitism pressure (% +/- 1 SE)
0
20
40
60
80
100
Redstart
Yellow W.
-12
-2
8
18
28
38
season day

Figure 7

Figure 8


other causes
para-sitism
pred-ation
Redstart
Yellow W.
daily mortality
building
egg laying
incubation
nestling
A:
B:
C:
D:
0.0
0.1
0.2
0.3
a
b
a,b
not parasitized
parasitized

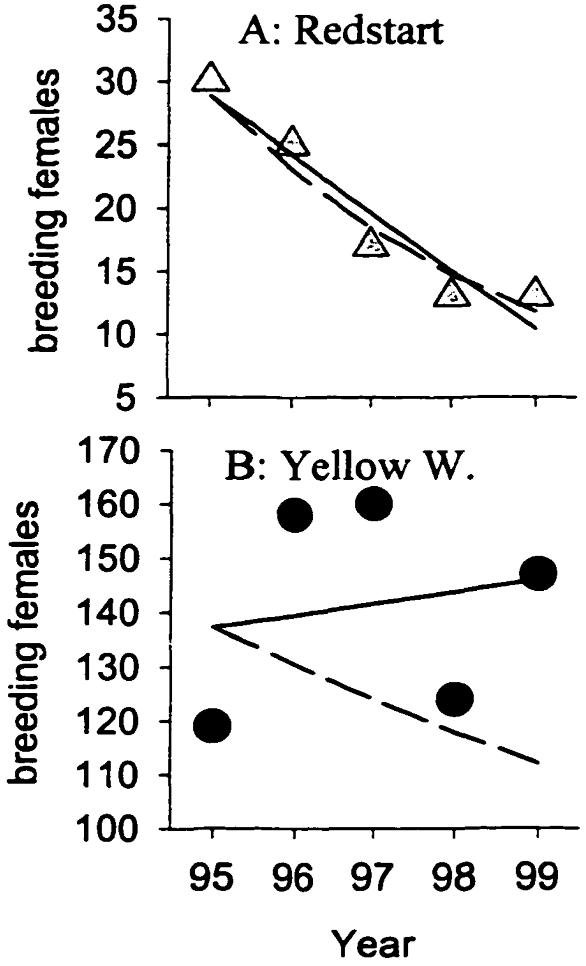

A: Redstart
breeding females
35
30
25
20
15
10
5
B: Yellow W.
breeding females
170
160
150
140
130
120
110
100
95
96
97
98
99
Year

Figure 9

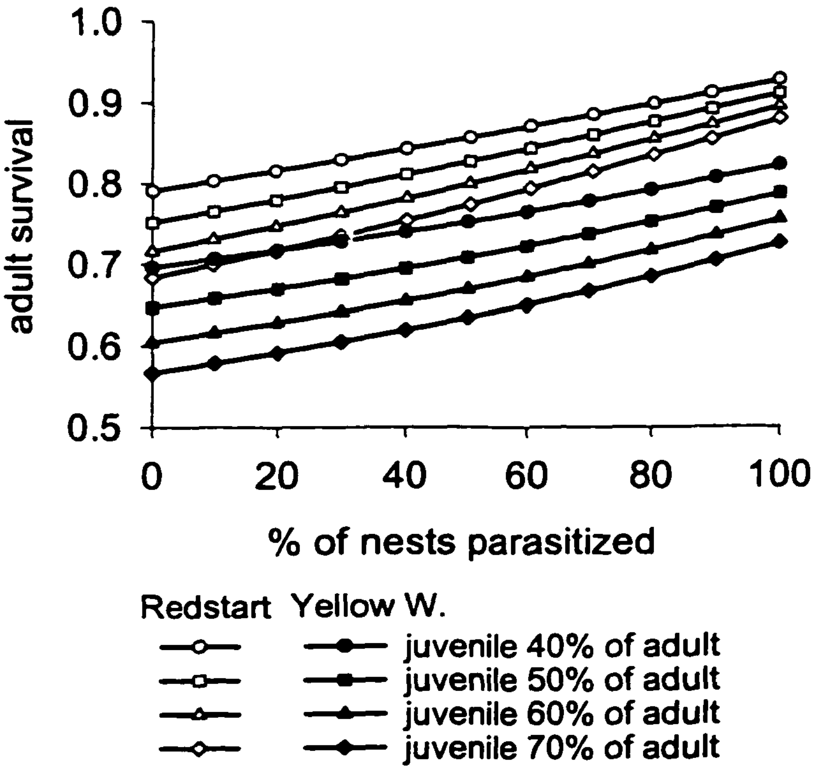
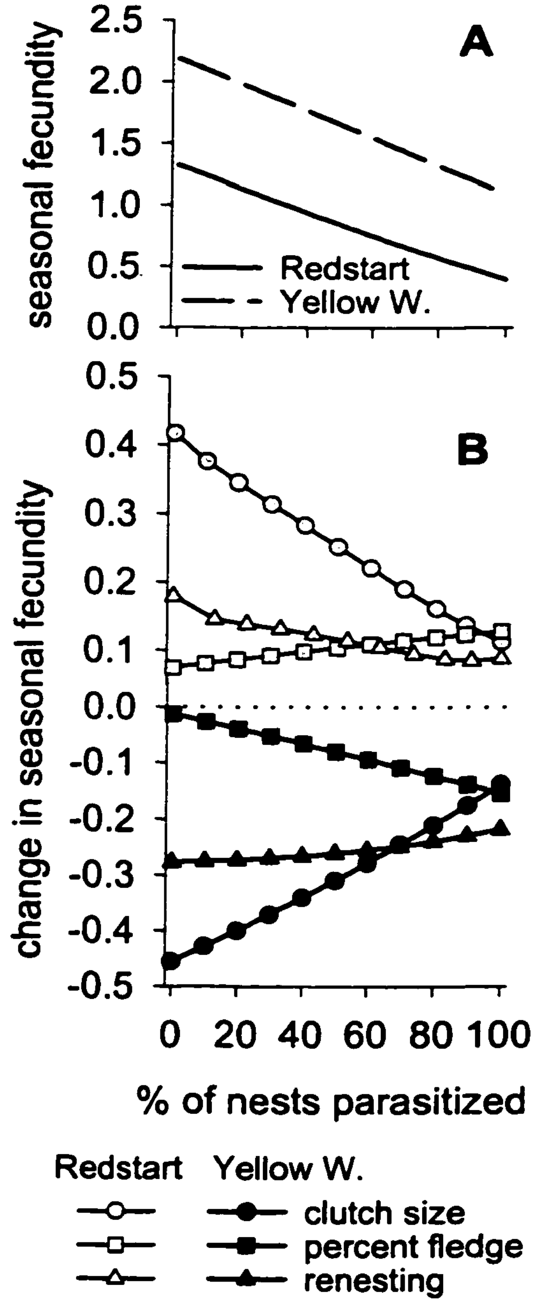

1.0
0.9
0.8
0.7
0.6
0.5
adult survival
0
20
40
60
80
100
% of nests parasitized
Redstart
Yellow W.
juvenile 40% of adult
juvenile 50% of adult
juvenile 60% of adult
juvenile 70% of adult

Figure 10

Figure 11


seasonal fecundity
2.5
2.0
1.5
1.0
0.5
0.0
A
Redstart
Yellow W.
change in seasonal fecundity
0.5
0.4
0.3
0.2
0.1
0.0
-0.1
-0.2
-0.3
-0.4
-0.5
B
0
20
40
60
80
100
% of nests parasitized
Redstart
Yellow W.
clutch size
percent fledge
renesting

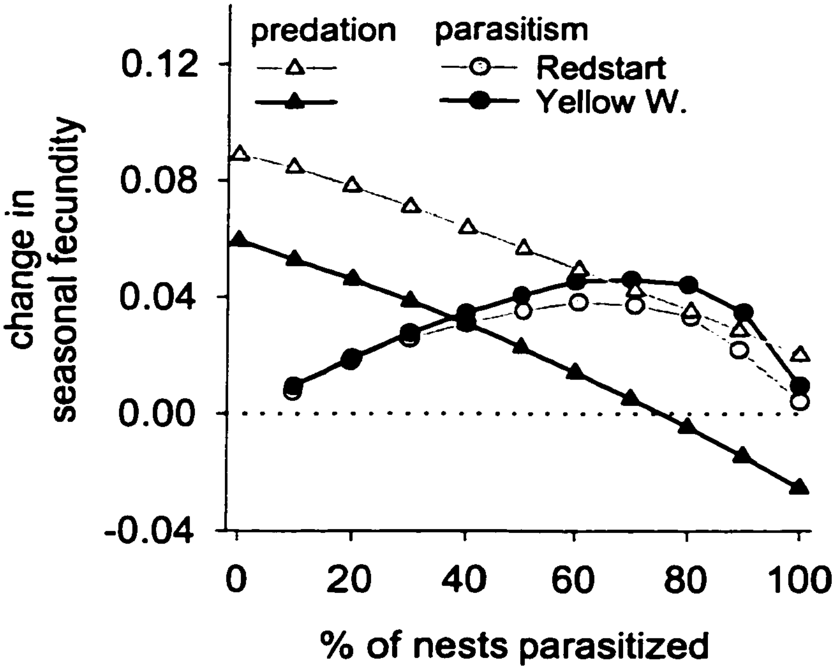

predation
parasitism
Redstart
Yellow W.
change in seasonal fecundity
0.12
0.08
0.04
0.00
-0.04
0
20
40
60
80
100
% of nests parasitized

Figure 12

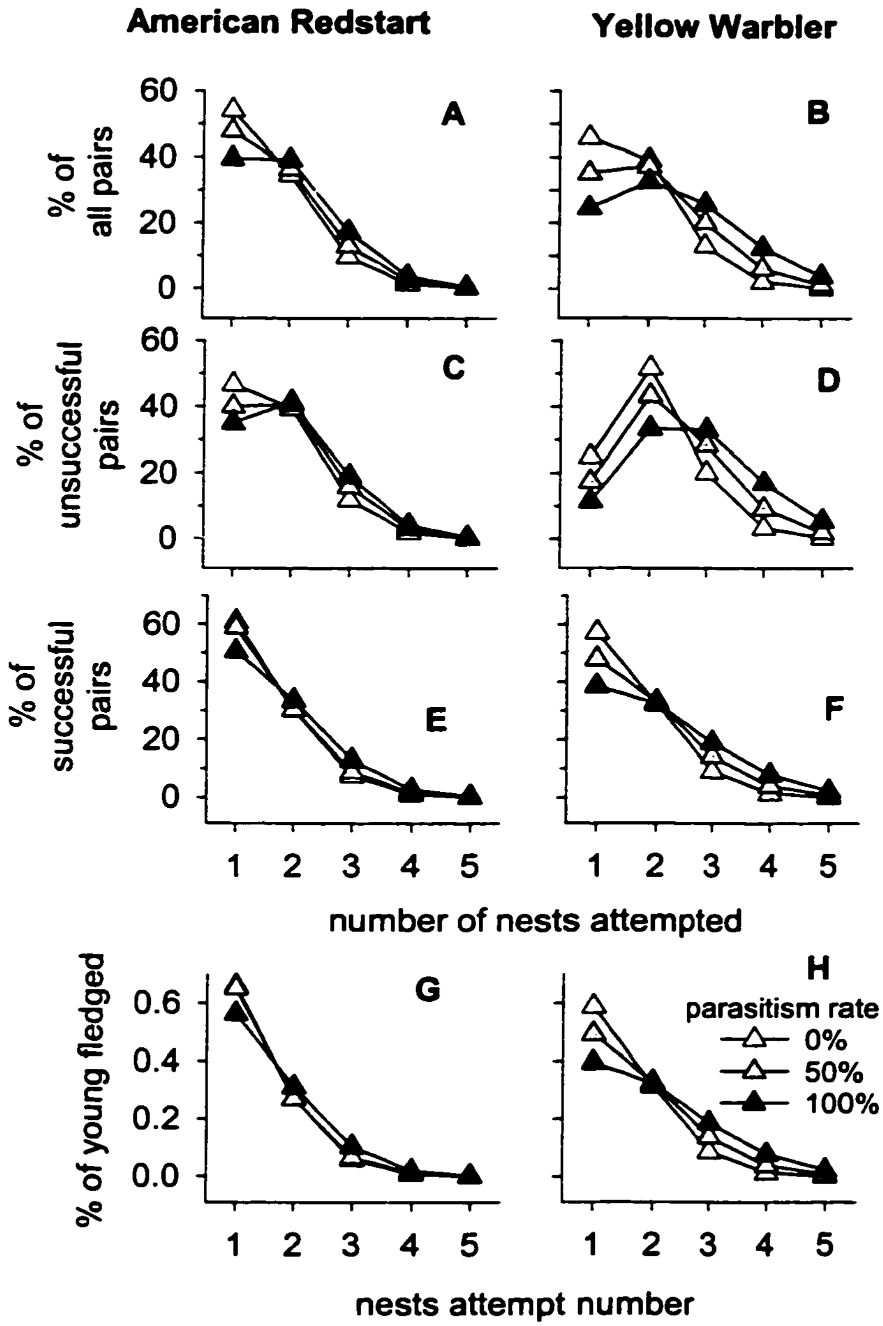

American Redstart
Yellow Warbler
% of all pairs
% of unsuccessful pairs
% of successful pairs
% of young fledged
60
40
20
0
0.6
0.4
0.2
0.0
A
B
C
D
E
F
G
H
1 2 3 4 5
number of nests attempted
nests attempt number
parasitism rate
0%
50%
100%

Figure 13