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DOES SHAPE MATTER? BREEDING
HABITAT USE AND REPRODUCTIVE
PERFORMANCE OF GRAY CATBIRDS
(DUMETELLA CAROLINENSIS) IN TWO
WESTERN WOODLAND HABITATS

Sharon Fuller

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DOES SHAPE MATTER? BREEDING HABITAT USE AND REPRODUCTIVE
PERFORMANCE OF GRAY CATBIRDS (*DUMETELLA CAROLINENSIS*) IN TWO
WESTERN WOODLAND HABITATS

By

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Thesis

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Does shape matter? Breeding habitat use and reproductive performance of Gray catbirds (*Dumetella carolinensis*) in two western woodland habitats

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Abstract

In the western United States, relatively few studies have comprehensively examined songbird performance in fragmented habitat, particularly within naturally fragmented systems. For this study, I used Gray Catbirds (*Dumetella carolinensis*) to distinguish differences in area use and reproductive performance in draw and floodplain habitat types, two spatially and physiognomically distinct deciduous woodlands. Naturally fragmented draw woodlands are bound by parallel hillsides, which creates a high edge-to-area ratio and a narrow, linear, configuration. By contrast, floodplain woodlands are wider and more contiguous. In this study, both draw and floodplain sites were surrounded by mixed-used grasslands and adjacent to each other, so they fell within the same landscape context and shared the same predominant, deciduous, species. However, these habitats differed according to configuration and floristics. To evaluate the potential effects of these differences, I monitored catbirds for three seasons (2014-2016) within both woodland habitat types. When compared to floodplain birds, results showed that draw birds had larger territories, exhibited lower daily nest survival rates, revealed delayed nest initiation patterns and had reduced fledgling success. I also tested local vegetation variables from surveys collected around the nest, to see if either configuration or local vegetation were potential mechanisms driving differential catbird productivity across habitat types. Tests of local vegetation showed that both down woody debris and mid-shrub canopy cover were significantly higher in draws than in the floodplains. However neither vegetation variable significantly influenced catbirds' daily nest survival rates, and therefore, did not support local vegetation as the driving mechanism. Evidence instead pointed toward configuration. Configuration likely influenced territory size in the draws, as the vegetation is constrained due to the long, thin, shape of this habitat type. Draw nests were also subjected to more depredation events than floodplain nests. This could also be explained by territory size, since larger territories require birds to cover and defend more area, which could affect nest vigilance. Additionally, draws may be saturated with predators due to the limitation of available woodland habitat, and predators may easily enter the habitat from edge interfaces. Thus, these results corroborate some studies in the eastern U.S. which have also shown negative impacts of increased edge and fragmentation on songbird breeding performance. Overall, this study's results can assist managers in understanding the repercussions of both natural and anthropogenically fragmented habitats, which will ultimately help manage breeding bird habitat in the future.

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INTRODUCTION

Habitat fragmentation currently poses one of the greatest threats to natural systems and wildlife populations (Wilson et al. 2016). While fragmentation is primarily caused anthropogenically by deforestation, agricultural practices and converting lands for human habitation, habitats can also be naturally fragmented through processes such as fire, significant weather events and topographic features (i.e. rivers or hillsides; Laurance et al. 2007). Habitat, in this study, is specifically defined by plant community, while habitat type, is defined through distinct “spatially and physiognomic differences” via Hutto, 1985. Given this definition of habitat, fragmented habitat types are generally limited in the amount of available vegetative structure for wildlife species and have higher edge-to-area ratios when compared to more contiguous habitats (Batary & Baldi 2004).

Fragmented habitats are varied in their shape or configuration. Particularly in the eastern United States, agricultural conversion has often created narrow, linear, strips of remnant woodland habitat (Hadley & Betts 2016). However, in the interior western United States where deciduous woodlands are rare (Knopf et al. 1988) and often naturally fragmented (Hejl 1992), habitats, such as draws, which are bound by parallel hillsides, share the narrow, linear, configuration with fragments in the east. This configuration has a high edge-to-area ratio (Batary & Baldi 2004). For songbird species which predominately breed in deciduous riparian woodlands (Knopf et al. 1988), the demographic impact of “edge effects” in these fragments may be an important ecological phenomenon.

Fragmentation and “edge effects” on songbirds have been studied extensively worldwide. Meta-analyses of these studies provide variable results (Lathi 2001,

Thompson et al. 2002, Vetter et al. 2013) yet, many studies have demonstrated negative “edge effects” on songbirds (Paton 1994, Andren 1995, Lathi 2001, Fahrig 2003, Vetter et al. 2013). Typically, songbird densities and overall biodiversity increase with proximity to edge (Strelke & Dickson 1980, Batary et al. 2014). Studies also document increased abundance and activity of nest predators correlated with increases in edge habitat (Paton 1994, Cox et al. 2012, Vetter et al. 2013). Areas with increased edge may even become saturated with predators and predators may easily access the habitat from multiple edges (Vetter et al 2013). Consequently, numerous studies have documented increased rates of nest predation associated with edge (Paton 1994, Niemuth & Boyce 1997, Reis & Sisk 2010, Klug et al. 2010, Cooper & Francis 1998, Banks-Leite et al. 2010). This predator-prey pattern with songbirds and edge is particularly true in the deciduous woodland and agricultural interfaces of the eastern and mid-western US (Paton 1994, Hartley & Hunter 1998, Lathi 2001, Thompson et al. 2002, Batary & Baldi 2004, Vetter et al. 2013).

In the western US, relatively few studies have looked beyond density to include comprehensive analyses of songbird reproductive performance in fragmented habitat or underlying mechanisms influencing songbird performance. One comprehensive study, conducted in western Montana, found that songbirds performed better in habitats adjacent to agriculture than to forested habitats and that predation decreased with increased agriculture in the landscape (Tewksbury et al. 1998 & 2006). These findings are in opposition to the paradigm of the eastern US. This contradiction, and the lack of comprehensive studies in the western US, warrant further study of songbird performance in areas with high edge. We also don't know if the anthropogenically induced “edge

effects” noted in the eastern US apply to naturally fragmented systems of the western US or if the natural shape of these habitats influence habitat quality for songbirds.

We can gain a comprehensive understanding of songbird habitat quality by studying songbird area use and breeding performance (Boves 2015, Stephens et al. 2015). While songbird density is generally accepted as a measurement of habitat quality (Blancher et al. 2007), Van Horne recognized in 1983, that studying density alone can sometimes be misleading. For instance, songbirds attracted to edges may show higher densities, but more predators in these areas may influence overall breeding success. In this instance, density alone would be a poor indicator because reproductive performance and habitat quality are decoupled. Therefore, Van Horne (1983) and Johnson (2007) suggested using density in combination with other measures of reproductive performance such as nesting success and productivity. In addition, studying bird pairs’ area use and territory establishment are also good indicators for assessing habitat quality. In fact, numerous studies have demonstrated that territory sizes are inversely related to resource availability (Smith & Shugart 1987, Ortega & Capen 1999, Kesler 2012). Within a species, pairs in areas with more resource abundance have smaller territories than pairs in areas with fewer resources (Kesler 2012). The timing of breeding may also be a good indicator of songbird habitat quality since birds often delay breeding in lower quality areas. These delays are generally attributed to greater predator activity (Byrkjedal 1980, Martin 1987, Kearns 2012) or reduced food availability (Martin 1992, Ortega & Capen 2002). Therefore, combining multiple measures of songbird reproductive performance can give a relatively comprehensive indication of habitat quality for that species (Van

Horne 1983, Johnson 2007). These indicators may also be used to compare songbird habitat quality between different habitats.

For this study, I examined two deciduous woodland habitat types with different shapes, in western Montana, to test for the effects of habitat configuration on songbird habitat use and reproductive performance. In this region, native deciduous woodlands are rare, making up <1% of the landscape. Much of these woodlands are found along floodplains, which represent relatively contiguous habitat, or in draws, which represent naturally fragmented habitats (Hauer et al. 2016). Floodplains consist of relatively wide strips of woodland habitat while draws are narrow and dominated by edge in comparison. In the study area, both floodplain and draw habitat types abut mixed-used grasslands and the two habitats are adjacent to each other, so they fall within the same landscape context. To compare differences between the two habitats, I chose Gray Catbirds (*Dumetella carolinensis*) as an indicator species, given their abundance and close association with deciduous woodlands in this region (Smith et al. 2011). They also demonstrate a strong edge preference (Keller et al. 1993, Peak & Thompson 2006, Keller & Yahner 2007). These factors make catbirds an ideal candidate to test the influence of configuration and habitat quality between floodplain and draw habitat types.

I compared habitat quality for catbirds between the two habitats via measures of habitat use and reproductive performance, including: territory size and pair density, nesting success, the phenology of nest initiation, and fledgling success. I also examined two potential mechanisms behind differences in catbird nest success within the two habitats: (1) habitat configuration i.e., reproductive performance is different due to the shape of the habitat (2) local vegetation at the nest site scale (microhabitat), i.e.

reproductive performance is different due to vegetative differences within the habitat types. My research hypothesis was that habitat configuration with more edge and less area would result in lower habitat quality for catbirds. I predicted the configuration of draws would result in lower nesting success and productivity, along with larger territory sizes due to the high amount of edge and resource distribution.

METHODS

Study Area

I conducted research on the MPG Ranch, located in the Bitterroot Valley, near Florence, MT. The MPG Ranch sits between the Sapphire Mountain Range to the east and the Bitterroot River, which flows along the western edge. The study area encompassed over 3,350 ha, consisting of a mosaic of deciduous woodlands and mixed-used grasslands (i.e., range, agriculture). I located 11 study sites in deciduous woodlands representing two different habitat types (Figure 1). Three floodplain sites consisted of relatively extensive patches of deciduous woodlands found along bottomland, adjacent to the Bitterroot River on one side and bordered by grassland on the other. The eight draw sites consisted of narrow, linear, strips of deciduous woodland bound by adjacent grassland slopes.

Dominant tree species within the study sites included Cottonwood (*Populus balsamifera*), and Aspen (*Populus tremuloides*) and dominant shrubs included Chokecherry (*Prunus virginiana*), Wood's Rose (*Rosa Woodsii*) and Mock Orange (*Philadelphus lewisii*). All sites were sampled in 2015 and 2016. In 2014, sampling was limited to one floodplain site and two draws.

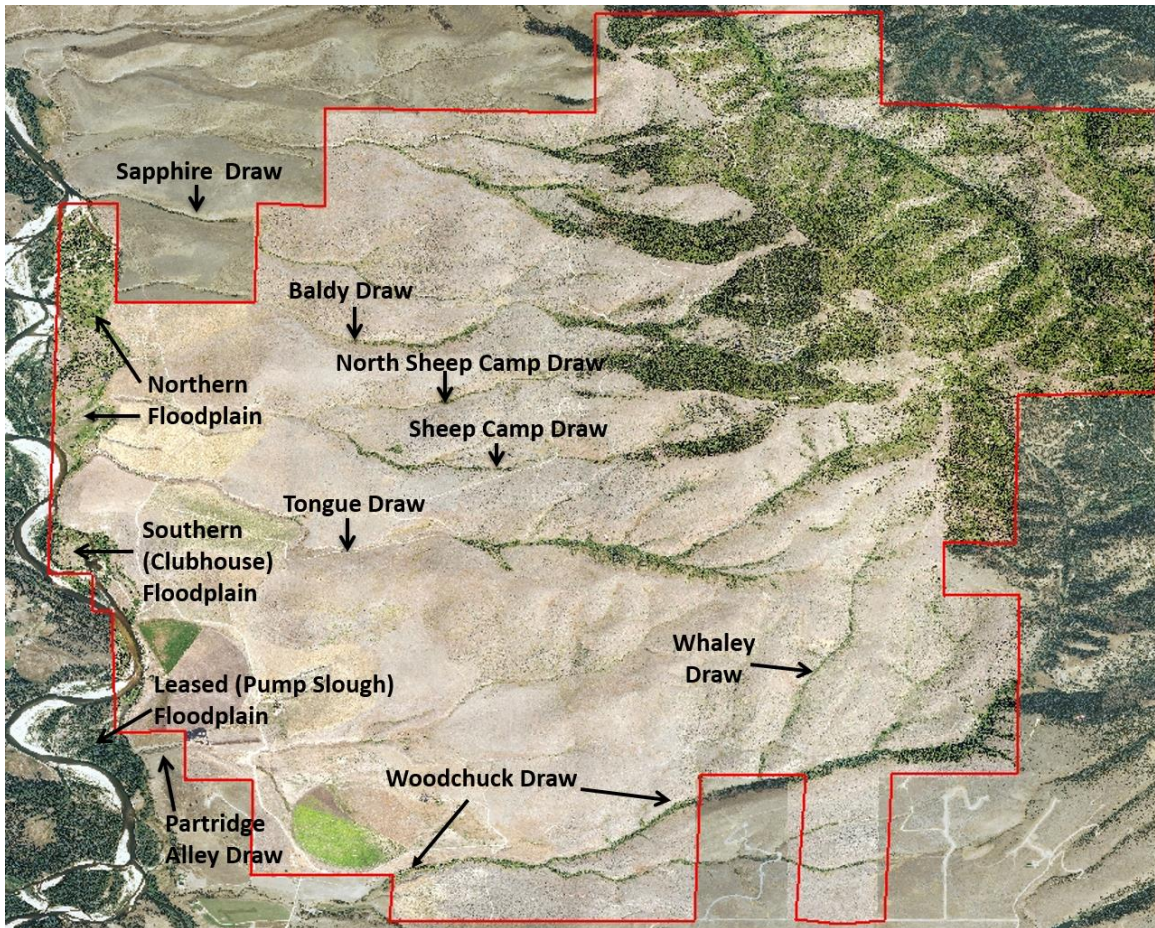


Figure 1. Study sites sampled from 2014-2016 at MPG Ranch (boundary outlined in red), MT.

Calculating edge-to-area ratios

To calculate edge-to-area ratios, I created polygons around each site in ArcMap GIS 10.4.1 and used the calculate geometry tool to generate the total amount of area (m^2) within each polygon. For edge calculations, I used the line tool to trace and quantify the total amount of edge (m) for each site. I then divided the total amount of edge by the total amount of area (m/m^2), for each site.

Marking and counting birds

To aid in identifying and tracking individuals, I banded all captured birds with unique color combinations. I used intensive mist netting efforts to mark catbirds at the

study sites during the breeding season, from the end of May to mid-July, each year. I prioritized capturing males and generally used target-netting efforts. Birds at the Northern Floodplain site were also passively captured during a MAPS summer banding station that ran every ten days at that site.

Territories and Density

To delineate territories, I used spot-mapping techniques (Martin & Guepel 1993). Spot-mapping was conducted at least once a week, for seven weeks, in each year. During spot-mapping sessions, I located and identified all marked and unmarked catbirds and recorded their movements and specific territorial or breeding behaviors (International Bird Census Committee 1970). I compiled all observations from spot-mapping sessions per year onto summary maps. Territories were defined by clusters of catbird observations indicative of territorial defense or breeding activity and spanning at least three visits. I defined a territory as successful if at least one fledgling was produced by the pair, as evidenced by observing fledglings or parental care of fledglings outside of the nest.

To estimate territory density, I divided the number of territories by the area of available habitat at each site. I designated “available” habitat, or habitat meeting general criteria for use by catbirds, as areas that had at least 10% cover of shrubs of at least 0.5 m in height. Areas that did not meet this criteria and constituted an area larger than the average catbird territory (0.64 ± 0.06 ha) were excluded. To calculate the size of each pair’s “total utilized territory” (Smith & Shugart 1987, Zach & Falls 1979, Ortega & Capen 2002), I transferred the spatial information for each of the 115 delineated territories into ArcMap GIS 10.4.1 and created individual shapefiles. I then used the

geometry tool in ArcMap to calculate the area for each territory via the minimum convex polygon method (Mohr 1947).

Reproductive Success

I measured differences in nesting success between the two habitat types using standardized methods to locate active nests from Martin and Guepel (1993). I searched for nests at each site at least two times per week and during spot-mapping sessions. I monitored active nests (with eggs or nestlings present) every three to four days and checked contents to determine the nest stage, age of nestlings, and fate. To determine the fate of each nest and to calculate nest exposure days (the number of days a nest was under observation), I used BBIRD's nest fate protocol (Martin et al. 1997).

To assess breeding phenology, I used nest card information to determine initiation dates (the first day of laying) for each initiated nest. The earliest initiation date within each year represented day 1 of the season. I used different starting dates each year since catbird arrival and nesting dates varied among the three years.

Local Vegetation

To assess vegetation composition and structure within available catbird habitat, I conducted surveys within nested circular plots centered on 86 nests. For each survey, I recorded vegetative variables within two nested circles of 5 m and 11.3 m radii (Martin et al. 1997). Within 5 m of each nest, I recorded percent ground cover and estimated percent canopy cover of shrubs in each of three vertical layers (0-0.05m, 0.05-3m, 3m+). Within 11.3 m of each nest, I counted snags and trees.

Data Analyses

For the response variables territory density, territory size, and nest initiation date, I used generalized linear models in program SAS (SAS 2013) to test for differences between habitat types. For all models, I included habitat type, year, and the habitat-year interaction. I excluded the interaction when it was not significant ($P > 0.05$). In cases when the response variable was positively skewed (i.e., territory size, nest initiation), I used a log-normal distribution. I also tested for local vegetation differences between the two habitats using generalized linear models in SAS. To determine differences, I tested each vegetation variable independently as a response variable, with habitat type as the explanatory factor.

To evaluate factors influencing differences in daily nest survival rates (DSR) between the two habitat types, I used logistic exposure models (Shaffer 2004) in R version 3.3.2 (R Core Team 2016). I included habitat type and year in these models. For the dependent variable, I used nest fate data from 86 nests and excluded one nest of unknown fate. To test whether habitat associated differences in local nest vegetation influenced survival, I ran a separate model that included only those vegetation variables that differed significantly ($P < 0.05$) between the two habitats. I ran additional models with habitat type and added the two vegetation variables along with day of initiation and year, to account for and hold these variables constant, to isolate the habitat type effect on the probability of daily nest survival rates.

To determine if the probability of nest success was influenced by initiation dates, I ran a logistic regression analysis in R. I used nest success as our response variable and initiation date and year as factors. I also used logistic regression (R Core Team 2016) to test whether the probability of fledgling success (a territory producing at least one

fledgling) differed by habitat type. I included year and the year x explanatory factor interaction in both of these models and excluded the interaction when not significant ($P > 0.05$).

RESULTS

Edge-to-Area Ratios

The average edge-to-area ratio for draw sites was $\bar{x} = 0.069 \pm \text{SE of } 0.004 \text{ m/m}^2$ and $\bar{x} = 0.01 \pm 0.007 \text{ m/m}^2$ for floodplain sites. Draws had significantly higher edge-to-area ratios when compared to floodplain sites ($F_{1,9} = 64.74, P < 0.0001$).

Territories and Density

Between 2014 and 2016, I color-banded 135 individuals and mapped 69 established catbird territories in floodplain habitat, along with 46 territories in draw habitat.

Territory densities did not differ significantly between habitat types, ($F_{1,1} = 0.88, P = 0.37$; Table 1). This result held when I excluded sites in which no territories were delineated ($F_{1,1} = 0.03, P = 0.9$; Table 1).

Table 1. Gray Catbird (*Dumetella carolinensis*) mean territory densities $\pm \text{SE}$ including all sites and used sites within draw and floodplain habitat

Habitat Type	All Sites	Used Sites
Draw	0.31 \pm .15	0.52 \pm .19
Floodplain	0.58 \pm .25	0.58 \pm .25

Across years, territories were significantly larger in draw habitat ($\bar{x} = 0.52 \text{ ha.} \pm 0.05$) relative to the floodplain habitat ($\bar{x} = 0.41 \text{ ha.} \pm 0.04$; $F_{1,109} = 3.98, P = 0.049$).

Reproductive Success

I monitored 86 nests across years, with a total of 59 floodplain and 27 draw nests.

Predation caused the majority of nest failures, implicated in 38 of 40 cases. Remaining

nests losses were due to Brown-headed Cowbird parasitism (n=1) and a potential parasitic insect event (n=1).

Nest initiation dates differed significantly between the two habitat types applied across years. The mean initiation date occurred on day $\bar{x} = 13.2 \pm \text{SE of } 2.8$ (Figure 2a), in the draws as opposed to $\bar{x} = 7.4 \pm \text{SE of } 1.01$ (Figure 2b) on the floodplain ($F_{1,80} = 5.38, P = 0.023$). The strength of the habitat effect varied significantly among years, as indicated by the interaction between habitat and year ($F_{1,80} = 3.32, P = 0.041$). In both 2014 and 2016, initiation occurred later in draw habitat ($\bar{x} = 17.4 \pm \text{SE of } 9.29$; $\bar{x} = 15.2 \pm \text{SE of } 3.71$) vs. on the floodplain ($\bar{x} = 0.49 \text{ ha.} \pm \text{SE of } 1.79$; $\bar{x} = 7.4 \pm \text{SE of } 1.32$). However in 2015, mean initiation occurred 1.9 days earlier in the draws ($\bar{x} = 10.1 \pm \text{SE of } 2.55$) than in floodplain habitat ($\bar{x} = 11.9 \pm \text{SE of } 1.96$).

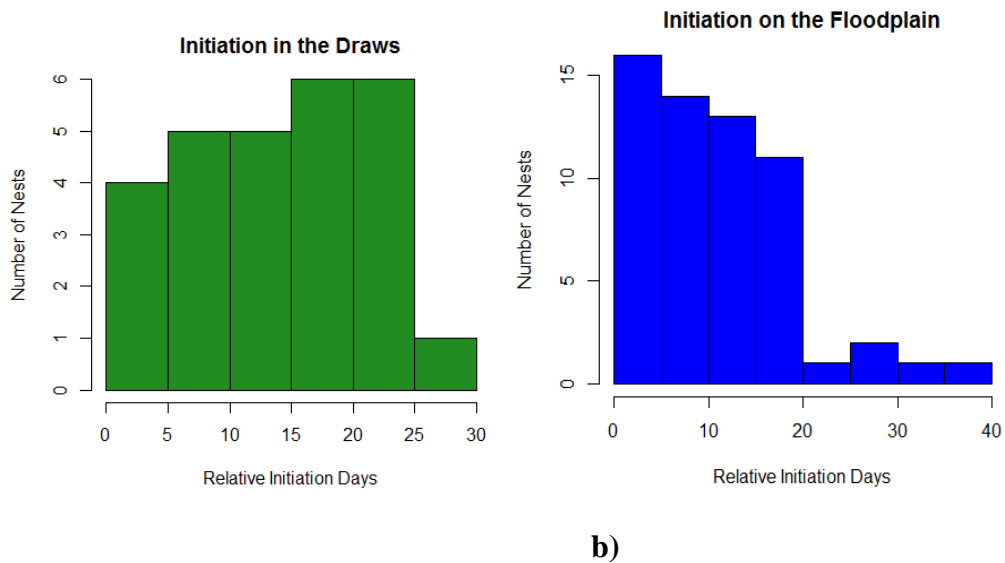


Figure 2 Relative nest initiation in a) draws and b) floodplain.

Catbird's nesting success decreased significantly with each added day of initiation ($z = 0.03, P = 0.013$; Figure 3). With each additional day, the odds of success decreased by 7% (95 % CI [14, 2]; Figure 3).

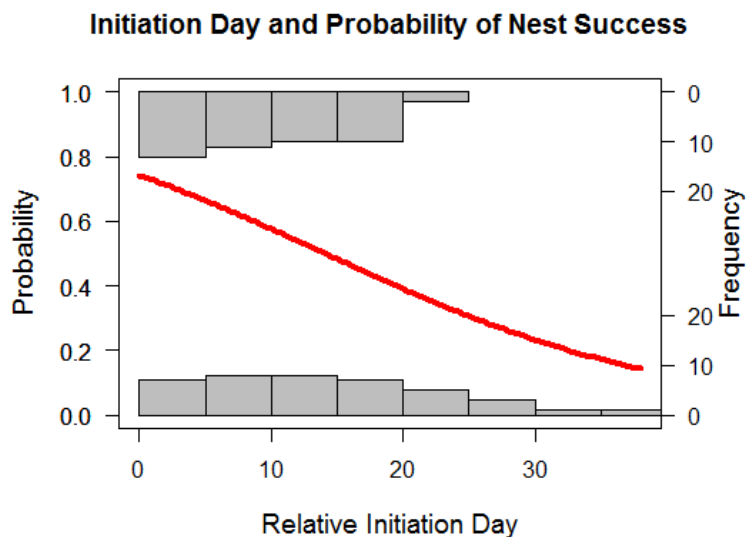


Figure 3: The relative day of initiation and probability of nest success. This histograms show the number of nests for each outcome and the red logistic line shows the probability of outcome according to the timing of initiation.

Daily Survival Rates

With my base logistic exposure model, inclusive of habitat type and year {Hab_Type + YR}, daily survival rates (DSR) were marginally lower for nests in draw compared to floodplain habitat ($z = -1.84$, $P = 0.054$).

I narrowed down the differences in local nest vegetation between the habitats to two variables. Both variables, downed woody debris (\bar{x} of $6.4 \pm 1.6\%$ vs. $2.7 \pm 0.5\%$) and mid-story shrub cover (\bar{x} $53 \pm 6.3\%$ vs. $39.3 \pm 3.2\%$) were significantly higher in draw vs. floodplain habitat ($F_{1,85} = 8.0$, $P = 0.006$; $F_{1,85} = 4.4$, $P = 0.039$, respectively). I ran these variables in a logistic exposure model to test if this vegetation difference may be a mechanism behind the difference in daily survival rates between habitat types. I first tested both variables together against fate, excluding habitat type {DEAD_DOWN + SHRUBC_L2}. Neither variable exhibited a significant effect on DSR ($P = 0.86$ and $P = 0.16$, respectively). When these habitat-related differences in vegetation were controlled

for in a model that included habitat type {Hab_Type + DEAD_DOWN + SHRUBC_L2}, the habitat effect was significant ($z = 2.53$, $P = 0.011$; Table 2). In this model, the maximum likelihood estimates show strong evidence of daily nest survival rates being lower in draw habitat ($\bar{x} = 0.87 \pm \text{SE of } 0.4$) than in floodplain habitat ($\bar{x} = 0.95 \pm \text{SE of } 0.55$). I also ran additional models controlling factors I knew could likely influence survival, including year and day of initiation {Hab_Type + DEAD_DOWN + SHRUBC_L2 + DAY_INIT + YR}. Here, the habitat effect remained significant, indicating lower likelihood of daily nest survival in the draw compared with floodplain habitat ($z = 2.15$, $P = 0.032$).

Similarly, using an AIC approach, the model including the two vegetation variables shows that accounting for these variables means lower survival in draw ($\bar{x} = 1.93 \pm \text{SE of } 0.55$) vs. floodplain habitat ($\bar{x} = 2.93 \pm \text{SE of } 0.39$; Table 2).

Table 2: Model results testing differences between draw and floodplain habitat types of Gray Catbird (*Dumetella carolinensis*) daily nest survival rates. Models include a base model with habitat type and year, a model with only vegetative differences between the two habitat types and a model with habitat type and local veg differences which could influence daily nest survival rates. Table includes degrees of freedom and AIC values for each model.

Model	df	AIC
Habitat_Type + YR	3	174.28
Dead_Down + Mid-Story_Shrub_Canopy + YR	3	175.42
Habitat_Type + YR + Dead_Down + Mid-Story_Shrub_Canopy	4	170.5

The probability of a territory fledging young was significantly lower in draw compared to floodplain habitat, with nearly a two-fold difference ($\bar{x} = 0.43 \pm \text{SE of } 0.12$ vs. $\bar{x} = 0.79 \pm \text{SE of } 0.06$; $F_{1,1} = 11.52$, $P = 0.001$).

DISCUSSION

My study, involving Gray Catbird area use and reproductive performance in western Montana, provided evidence that naturally fragmented woodland draws were lower quality habitats for catbirds compared to floodplain habitats. Overall, this work addresses the lack of comprehensive studies looking at naturally fragmented habitats within this geographic region and whether the “edge effects” documented in the eastern US on songbird performance applies to habitats with similar shape and more edge, in the western US. I looked at several measures to assess catbird habitat quality within floodplain and draw habitat types. Overall, draw birds held larger territories, exhibited a prolonged initiation pattern, had lower daily nest survival rates, and manifested lower fledging success. All of these factors pointed in the same direction, suggesting that draws represented lower quality habitat for catbirds compared to floodplains. I also examined two potential mechanisms behind the observed differences in metrics for catbird habitat quality: 1) habitat configuration and 2) local vegetation. Based on the results, I suggest habitat configuration as the overall driving mechanism behind observed differences in catbird habitat quality between the two habitats.

Territories and Density

In this study, territory density estimates did not provide evidence that catbirds avoided draw habitat, regardless of whether I included all sites or excluded sites with no observations of catbirds. Other studies have also found that catbirds are shrub generalists and will breed as long as dense, shrubby, vegetation is present (Dowd 1992). However, Van Horne (1983), warned against relying on density alone to evaluate habitat and encouraged comprehensive analyses to more accurately identify lower quality habitats or

even “ecological traps”-- where birds preferentially or are equally likely to settle into areas that consistently exhibit lower productivity over more successful habitats (Robertson & Hutto 2006). In this study, while density results alone gave no indication of differences between habitat types, other measures, such as territory size, provided evidence of discrepancies in quality between the two habitats.

In all three years, I observed significantly larger territories in the draws compared to floodplain territories. Studies show that the size of a territory is often inversely correlated with resource abundance (Smith & Shugart 1987, Ortega & Capen 1999, Kesler 2012). Since draw birds held larger territories, this could suggest that draw habitats had fewer resources compared to the floodplain. However, results comparing local vegetation differences between the habitat types did not demonstrate this. In fact, analyses demonstrated that both down woody debris and mid-story shrub cover were significantly higher within draws compared to floodplain habitats, while all other local vegetation variables exhibited no differences between habitat types.

Another explanation for larger territory sizes in draws could be that their narrow and linear configuration provide less available habitat per unit area on the landscape when compared with floodplain habitats. Thus, the elongated shape of draw habitats constrains resource distribution, which may force birds to establish larger territories in draws (Kesler 2012).

Reproductive Success

Fledgling success rates differed significantly between the two habitats as draw territories were almost two times less likely to produce fledglings than floodplain territories. My initial analysis of daily nest survival rates also provided evidence of lower

daily nest survival rates for nests in draws compared with the floodplain, albeit this was marginally significant ($P=0.054$). However, when I added differences in local vegetation into the model, to control for differences that could influence daily nest survival rates, the habitat effect became stronger, indicating significantly lower daily nest survival within draw habitats.

I also observed an overall pattern of later nest initiation in the draws than on the floodplain. Studies have demonstrated the strategic timing involved in songbird breeding performance (Martin 1987, Ortega et al. 2006). Ideally, birds are in sync with their surroundings and time their nesting activities when food availability (Ortega et al. 2006) and energetic demands are highest (Martin 1987). Studies specifically examining the onset of breeding (i.e. initiation of first nests) have shown that increased food availability promotes earlier breeding while reduced resources cause delays (Martin 1987, Ortega et al. 2006). In this study, since local vegetation analyses did not indicate vegetative resources were lower within draw habitat, it is unlikely that resources are influencing the differences in initiation patterns. Additionally, if local vegetation drove the observed differences in nest survival, I would expect controlling for vegetative differences would mask the habitat effect, but this was not the case. Instead, it demonstrated a distinct difference in nest survival between the two habitats.

According to the protocol I used to determine nest fate (Martin et al. 1997), most nests failed due to depredation events, which is a common pattern seen across open-cup nesting songbird species (Martin 1993). In line with this research, the prolonged initiation pattern within draw habitat may be indicative of increased levels of renesting in response to elevated depredation rates. Additionally, lower reproductive performance in

draw habitats could be explained in terms of decreases in nesting success that are correlated with later nesting attempts. Many studies have demonstrated this correlation between later nesting and the increased probability of failure due to predation (Martin 1987, Martin 1992, Ortega & Capen 2006). Consistent with other studies, the probability of catbird's nesting success diminished with each additional day of initiation. Nest attempts later in the season may also coincide with greater predator abundance given that predators have their young. Thus, increased depredation events provide one likely explanation for greater nest failure during this time.

However, such explanations do not address why differences in predation rates between the two habitat types occur in the first place. Results from this study suggest the answer does not reside in the differences between local vegetation in draw and floodplain habitats driving differential productivity and nesting success rates. This was evident when I tested and controlled for local vegetative differences between the two habitat types and nevertheless found significantly lower daily nest survival rates (DSR) in draws compared with floodplains. This suggests that, since differences in vegetation did not significantly influence DSR, differences in DSR between habitat types are due to some other mechanism beyond local vegetation. Thus, a superior mechanistic explanation for lower productivity and nest survival within draws may well appeal to the particular configuration of high edge and narrow strips of vegetation associated with this habitat.

This appeal to territory configuration coheres with previous research. Numerous studies have found that typical nest predators concentrate near edges (Chalfoun et al. 2002, Cox et al. 2012, Vetter et al 2013). Generalist predators may also be more inclined to use the abrupt interfaces of edges as travel lanes (Cavitt & Martin 2002, Thompson et

al. 2002, Tewksbury et al. 2006). The predators using these lanes can easily penetrate into the habitat from either edge, running along draw habitat, and either intentionally or incidentally depredate nests (Vickery et al. 1992, Vetter et al. 2013). The narrow configuration of draw habitat may also funnel predators (Tewksbury et al. 2006) and increase foraging efficacy as predators have less immediate area to peruse. The present study might be viewed as a contribution within this more general research framework.

Conclusions

Throughout this study, catbirds showed greater area use and lower reproductive performance in naturally fragmented draws compared to floodplain habitats. Density results proved to be a misleading indicator of habitat quality, as catbird densities did not suggest that catbirds avoid draws despite evidence of lower performance within draw habitat. These findings align with Van Horne's (1983) call to approach density, as an indicator, with caution. Results also suggest that study designs should include density, along with a comparative measure of productivity, to accurately identify the overall quality of a habitat (Van Horne 1983, Johnson 2007, Cox et al. 2012).

Additionally, these findings may suggest that draws could function as an "ecological trap" (Robertson & Hutto 2006). However, additional years of data and a larger sample size would be needed to appropriately confirm this.

In draw habitat, catbird reproductive performance was significantly lower, which could stem from greater predator activities and abundance associated with this particular habitat type (Chalfoun et al. 2002). If differences in local vegetation variables between the two habitats were attracting or enhancing predator activities, then I would have

expected these variables to influence daily nest survival rates. However, the analyses of local vegetation did not support this.

By contrast, several indicators supported habitat configuration as a likely driver of differences in catbird performance between habitat types. Evidence included larger territory sizes and lower reproductive performance, which is likely due to constrained resource distribution. In general, larger territories require birds to travel farther to provide for themselves and their young, thereby increasing the amount of edge a bird must defend (Kesler 2012). These factors require more time away from nesting duties, which may ultimately reduce nesting vigilance and increase the risk of predation (Martin 1992).

Predator activities also likely affected overall initiation patterns and overall nesting success within the draws. Multiple studies demonstrate increased nest predator activities and abundance are associated with edges in fragmented habitats (Chalfoun et al. 2002, Thompson et al. 2002, Vetter et al. 2013). Since draw habitats contain more edge than area, due to their configuration, these edges may attract relatively more predators than floodplain habitat. Additionally, edges can provide travel lanes for generalist predators which can allow easy access into the habitat, or the narrow habitat may concentrate predators and funnel their movement patterns.

All of these findings demonstrate how draw configuration, with a narrow, linear, shape and relatively more edge, could explain differences in catbird performance within these naturally fragmented habitats.

Future research

Overall, it is important to understand, in general, the extent to which bird communities are impacted by naturally fragmented areas and how the shape of these fragments, particularly with more edge, influence songbird reproductive performance. This is especially important considering that birds may inherently demonstrate lower performance in habitat configurations with more edge, whether natural or unnatural. However, not all fragments are equal (Thompson et al. 2002) and therefore, studies provide varied conclusions on fragments and increased edge (Lathi 2001, Batary & Baldi 2004, Knowton et al 2017). This variation likely stems from different predator communities within different study areas (Cavitt & Martin 2002, Chalfoun et al. 2002). Thus, to appropriately address what drives differences in songbird habitat quality across study areas, we need to identify who the predators are (Chalfoun et al. 2002). More comprehensive studies are also needed to understand to what extent the results from this study apply across naturally fragmented systems, and whether they apply to habitats with similar configurations, particularly in the west. In addition, more comprehensive studies are needed to understand how different species with different nesting preferences (i.e., ground or cavity nesters) and different species which may be sensitive to additional edge effects, such as parasitism by Brown-headed cowbirds, are impacted by this particular configuration.

Management Implications

If managers want to promote optimum habitat for the greatest diversity of songbirds, they should focus on identifying and managing the predator community (Chalfoun et al. 2002). Efforts should concentrate on what attracts or promotes these predators in fragmented systems and how they're affecting songbird populations.

Managers also need to keep in mind how songbird habitat quality is assessed. Comparing comprehensive measures of songbird performance between different areas will give the best indication of habitat quality for these birds.

Lastly, it is important to note that preserving narrow strips of high quality land may not inherently produce high quality habitats.

As habitat fragmentation continues, it remains important to understand the impacts of fragmented habitats and the influence of increased edge in managing habitats for songbirds in the future.

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