INTRINSIC AND EXTRINSIC FACTORS PREDICT LOCAL RECRUITMENT AND NATAL DISPERSAL DISTANCE IN A RESIDENT PASSERINE, THE EASTERN BLUEBIRD (*SIALIA SIALIS)*

A Thesis
by
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Abstract

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Natal recruitment and dispersal distances can have important impacts on population dynamics and are influenced by ecological and individual factors. I assessed the intrinsic and extrinsic determinants of local recruitment and natal dispersal from a 3-year study of the breeding ecology of eastern bluebirds (Sialia sialis) in the mountains of North Carolina. Predictors included: offspring sex and body condition, year and seasonality of nesting, and estimates of habitat quality and nest site availability. Offspring were more likely to recruit and dispersed shorter distances when there was greater availability of nestboxes near their natal area. Further, bluebirds that weighed less for their skeletal size were more likely to recruit after fledging from territories with lower percentage of open pasture and grasslands and closer to forest edges, which may be explained by predation pressure following fledging. Alternatively, heavier bluebirds were more likely to recruit when fledged from more open territories but tended to disperse further; this may be explained by competition for nesting sites rather than predation pressure. Overall, dispersal in this species is influenced jointly by intrinsic and extrinsic factors suggesting that the interaction of individual quality, predation, and competition likely shapes natal philopatry in resident passerines.

Key words: recruitment, natal dispersal, non-migratory bird, eastern bluebird, post-fledging survival, competition

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Dedication

I would like to dedicate this work to my parents, Tracey Bly Shotwell and Charlie Hill. They have never doubted my capabilities and choices within my educational journey and have done everything in their power to ensure that I've got a hand to hold as I walk down my chosen path. Their support through my undergraduate degree and graduate school has brought me to where I am today, and I only dream of being able to repay them one day. Thank you both.

Table of Contents

List of Tables

List of Figures

Foreword

This thesis will be submitted to *Frontiers in Ecology and Evolution*, a peer-reviewed scientific journal published by Frontiers Media SA; it has been formatted according to the style guide for that journal.

Introduction

Recruitment and dispersal can have profound impacts on gene flow and help researchers understand the population dynamics of species (Hanski, 1999; Nichols and Hines, 2022). Natal recruitment – when a pre-productive animal remains in their natal habitat to breed for the first time – is particularly important because survival in juveniles tends to be both lower and more variable than in adults (Gaillard et al., 2000; Gaillard and Yoccoz, 2003). The factors that predict natal recruitment, or philopatry, vary between species and even within a species in different environments (e.g., Gowaty and Plissner, 1998; Becker and Bradley, 2007; Lang, 2013). It is therefore essential to integrate environmental and individual characteristics to gain a better understanding of how these predictors influence population dynamics across species and populations (Francis, 2006).

Although some studies assume natal recruitment is a proxy for post-juvenile survival (e.g. Rodríguez et al., 2016), certainly some individuals disperse beyond the area studied. Additionally, natal dispersal distance (the movement between the natal site and the site of first reproduction) is negatively correlated to the probability of local recruitment (Schaub et al., 2012). Yet, it is possible for animals to recruit to the natal fieldsite but to disperse relatively far because of competition for breeding sites. The hurdles involved in recruitment include achieving independence, survival to breeding age, returning to natal grounds, making the choice to breed there, and overcoming competition to acquire a territory (Becker and Bradley, 2007).

It is widely understood that natal dispersal is sex biased, with male mammals and female birds dispersing farther (Greenwood, 1980). Moreover, within passerine birds, recruitment rates are higher for resident (median = 6.3%; range: 0-39%) compared to migratory species (median = 2.6%; range: 0-13.5%; Weatherhead and Forbes, 1994). In both, recruitment rate is influenced by the intense three-week period post-fledging in which the juvenile mortality rate ranges from 23-87% (Cox et al., 2014). However, even within non-migratory populations, quantifying recruitment and dispersal is challenging in small-bodied and highly mobile passerines because one must track marked individuals between life stages.

Predictors of recruitment can be broken down into two classes; intrinsic factors, those that arise from within an individual, such as sex, body condition or inbreeding avoidance, and extrinsic factors, such as habitat or environmental factors (Cava et al., 2016). A combination of intrinsic and extrinsic factors predicts natal philopatry in great tits (*Parus major*); the probability of natal recruitment increases with fledgling size (tarsus length) and when birds fledge in the middle of the breeding season (Monrós et al., 2002; Rodríguez et al., 2016). In tree swallows (*Tachycineta bicolor*), conspecific density is an important social cue; females that fledge from higher-density disperse shorter distances as a result of increased perceived habitat quality (Carle-Pruneau et al., 2022). Both habitat and social factors predicted the probability of local recruitment in red-backed shrikes (*Lanius collurio*). Nestlings are more likely to recruit from large broods and from areas with frequent land management where they have higher foraging success, while parental quality, nest timing, and predation pressure do not predict recruitment in red-backed shrikes (Müller et al., 2005).

For species that nest in grasslands or grassland-forest edges, much native habitat has been replaced by fragmented and intensively managed agricultural lands including hay and pasture or by park or residential lands that are mowed frequently (Hannah et al., 1995). Researchers suggest that varying levels of anthropogenic activity is a primary cause of fluctuating population dynamics between nest sites (Cava et al., 2016). Thus, predictors of grassland recruitment are becoming more prevalent in the field of avian population dynamics. In the grassland nesting savannah sparrow (*Passerculus sandwichensis*) – a short distance migrant, natal philopatry is greater for nestlings hatched later in the season and for those with fewer opposite sex siblings (Cava et al., 2016). Although the effects of sibling sex ratio suggest selection to avoid inbreeding or competition for territories, nesting time was likely related to hay harvesting, thus Cava et al.'s (2016) study suggests both biological and human-induced influences on local recruitment. Researchers conducting a similar study on an island population of savannah sparrows found much higher natal recruitment rates in general, and that philopatric males recruited significantly more offspring than naive males (raised outside of the study area). Further, Wheelwright and Mauck (1998) found that of over 1000 breeding attempts, and many opportunities to pair with kin, no individuals bred with close relatives.

The impact of intrinsic factors like fledge date and body condition is apparent in some studies of passerines (Newton, 1989; Monrós et al., 2002; Rodríguez et al., 2016) while others show no influence on recruitment (e.g., Moreno et al., 2005). Body condition (mass) is not associated with natal recruitment in bobolinks (*Dolichonyx oryzivorus;* a grassland-nesting, long-distance migrant); however, those that fledge earlier in the season are more likely to recruit and philopatric mothers tend to produce philopatric offspring (White et al. 2021). Intrinsic and extrinsic predictors can also vary with year; the same research group did not find significant predictors of bobolink local recruitment a few years prior (Cava et al., 2016). While Cava et al. (2016) found weak positive relationships between recruitment, breeding density, and breeding success, they acknowledge that recruits probably go unnoticed due to the limitations of finding nests and capturing adults (Cava et al., 2016).

Such error can be reduced by studying box nesting species because nearly all nests can be found and monitored, individuals are easy to follow between years, and researchers can use historical box occupancy rate as a proxy of habitat quality (Jones et al., 2014). I assessed the intrinsic and extrinsic determinants of local recruitment by following breeding eastern bluebirds (*Sialia siali*s) for 3 years in the mountains of North Carolina. Eastern bluebirds are obligate secondary cavity nesters, with the majority of individuals in the region using man-made nestboxes rather than tree cavities (author, pers. obs.). Bluebirds are partial migrants such that northern populations migrate while southern populations are resident; it is likely that the bluebirds in western North Carolina are non-migratory (Gowaty and Plissner, 1998). However, some high elevation birds might migrate short distances to lower elevations with warmer climates; at least some of the marked individuals in the study population overwinter at the fieldsite (L. Sieffeman, pers. comm.). Bluebirds nest in or near open fields, where they mainly forage on ground arthropods during the breeding season and use a perch-to-ground foraging technique ~ 80% of the time (Gowaty and Plissner, 1998). In the population that I followed, box occupancy is positively associated with both habitat openness (percent grassland) and the number of fledglings produced annually (Jones et al., 2014), suggesting that bluebirds are attracted to nesting locations with greater grassy areas for foraging. This reliance on open grasslands for foraging makes bluebird habitat requirements very similar to the previously discussed grassland species. However, they are likely more limited by nestbox presence rather than food availability (Miller, 2010). Territory acquisition is a fundamental part of recruitment (Becker and Bradley, 2007) which is influenced by both intraspecific and interspecific competition (Parren, 1991). Tree swallows are the most common competitor for nesting sites at this field site, occupy nearly equal shares of the field site, also prefer open habitat (Nelson, 2022) and will usurp bluebirds from nestboxes (author, pers. obs.). Survival can affect recruitment as well; indeed, in the weeks immediately post fledging, juveniles move to locations close to forest edges which reduces predation rates (Jackson et al., 2011). Thus, both competition with conspecifics and survival may influence relationships between territory openness, recruitment and dispersal distance of bluebirds.

Natal recruitment in eastern bluebirds has been quantified in multiple locations and in the same location at different times. Recruitment varied between two non-migratory populations in the 2000s; 10% in South Carolina and only 1% in Georgia (Lang, 2013) while the South Carolina population had higher recruitment in the 1980s at 14.6% (Plissner and Gowaty, 1996). Moreover, in the South Carolina population, dispersal distance was greater for males in the 1980s but similar for males and females in the 2000s (Plissner and Goway, 1996; Lang, 2013). Hatch date also influenced post fledging survival and natal dispersal distance; those that fledged early in the season were less likely to survive to 40 days post fledging (Jackson et al., 2011) and dispersed nearly twice as far as those from later broods (mean of 1146m versus 620m; Lang, 2013). Further, Lang (2013) found that individuals from later broods remained closer to their natal nest but only when they were in good body condition (high ratio of weight to tarsus length).

In the Western NC population of bluebirds, I predicted that two intrinsic factors influence natal philopatry. First, I predicted that males would have higher rates of natal recruitment and shorter dispersal distances than females (Plissner and Gowaty, 1996; but see Lang, 2013). Second, I expected birds that were heavier for their skeletal size would be more likely to recruit to the natal population or exhibit shorter dispersal distances (Claramunt, 2021). I also predicted that three extrinsic variables influence philopatry. First, I predicted that birds would be more philopatric or disperse shorter distances when there was greater nestbox availability near their natal nestboxes. Second, I expected that recruitment would be positively associated with habitat quality as measured by a) historical occupancy (Jones et al., 2014) and b) land use characterized by open habitat in combination with close forest edges (Jones et al., 2014; Jackson et al., 2011). Further, if competition with more experienced bluebirds and tree swallows influenced dispersal, dispersal distance would be greater for juveniles fledged from high-quality habitats. Third, I expected fledglings that hatched from late-season broods would be more likely to recruit or disperse shorter distances compared to those hatched from early-season nests (Lang, 2013).

Methods

Field Methods

The field site consists of about 160 nestboxes dispersed over ~500 ha of observed bluebird nesting habitat near Meat Camp, NC (36.2996° N, 81.6765° W; **Figure 1**), and about 100 nestboxes dispersed over ~300 ha of observed habitat in Valle Crucis, NC (36.2093° N, 81.7784° W; **Figure 2**). Though the sites are spatially segregated by ~15km, they have very similar landuse. Both sites are composed of hay fields, cow pasture, recreational parks, and residential areas. Further, neither site has experienced major development since nestbox monitoring began. During the 2019-2022 breeding seasons, nestboxes were monitored weekly at the first sign of bluebird activity (early March). Female bluebirds lay one egg per day until a final clutch of 4-6 eggs, followed by a 14-18 day incubation. Once hatched, offspring remain in the nest for ~14-18 days supported by bi-parental care until fledging. Fledglings typically remain in family groups for up to 3 weeks post fledging, aside from late season fledglings which may remain with their family groups overwinter (Gowaty and Plissner, 1998).

Once egg laying began, boxes were monitored to determine first egg date, clutch size, hatching date, and brood size. At the field site, each breeding pair typically attempts two broods, therefore, each nest was classified as early (0) or late (1) based on whether egg laying occurred before or after May 25th. This date represents the natural break in timing between first and second nests in this population. At age 14 days post-hatch (DPH), nestling mass (+/- 0.01g) and tarsus length (+/- 0.01mm) were measured and nestlings were fitted with bands. Because bluebirds reach 81.7- 88.1% of adult mass (females and males respectively) and 100% of their tarsus length by 14 DPH, this age is considered an accurate representation of fledging mass and skeletal size (Gowaty and Plissner, 1998). Body condition was estimated as the ratio of offspring mass to tarsus length (Brown, 1996). Body condition indices must be used cautiously as they are indicative of fat and protein contents which vary seasonally and throughout breeding cycles (Schamber et al., 2009). Further, on 14 DPH, or when primaries are unsheathed to a significant length, feather samples were obtained from the fifth primaries to later determine sex by plumage coloration (Pinkowski, 1975).

Adult bluebirds were captured with nestbox traps while feeding nestlings and were fitted with a combination of USGS bands and color bands for identification in the field. If a bird was attempting a second or third brood of the season, and could be identified by color bands, capture was not attempted. Breeding birds were classified as returned (adults that were captured and banded in a previous breeding season at the field site), recruited (adults that were banded previously as nestlings at the field site), and naive (breeding birds that were unbanded upon capture). To calculate adult capture success rate, the percentage of captured adults out of total adults from *hatched* nests was determined per year.

Habitat Quality

I calculated habitat quality in two ways: via territory land use and historical occupancy rates at the field site. Territory quality via land use was quantified by taking into consideration the preferred habitats of both adults and nestlings. Using ArcGIS Pro 2.8.7, I imported data derived from satellite imagery at 10m resolution (Karra et al., 2021). The Land Use Land Cover (LULC) layer was overlaid onto nestbox GPS data (collected 2021). I created a 100m radius buffer around each nestbox to represent a typical bluebird feeding territory (Gowaty and Plissner, 1998). Within that buffer, I calculated percent openness as the summation of percentage rangeland and percentage cropland (**e.g., Figure 3**). I performed a raster to polygon function to convert the LULC data to a forest polygon layer. Using the near tool, I calculated linear distance (meters) to the nearest forest edge for every nestbox – a representation of distance fledglings would have needed to travel to find cover.

Historical occupancy was quantified following the methods of Jones et al. (2014) taking advantage of historical field site data. Occupancy was calculated as the number of years occupied by bluebirds out of the total years that the nestbox was available from 2009-2018.

Natal Dispersal Distance and Habitat Availability

I used ArcGIS Pro to determine the average natal dispersal distance (NDD) in the population. I created two layers from point data of natal nestboxes (natal) and recruited nestboxes (new). The two layers were merged using the merge tool. Next, I used the point to line tool to connect points based on nestling band ID. This function returned the arc length (°) of each line. That layer was then projected to PCS - WGS_1984_UTM_Zone_17N (UTM zone for Western NC). Unit conversion via reprojection yields the linear distance between the new and natal box in meters.

Within the typical dispersal distances, I calculated the availability of nestboxes close to the nesting sites of recruits in the year after hatching. I derived availability data from the historic occupancy datasets of both bluebirds and tree swallows. I used the average natal dispersal distance at the fieldsite to survey a 1740m radius for the number of available nestboxes during each fledgling's second year (**e.g., Figure 4**). For recruited bluebirds that bred within 1740m of their natal nest, an additional available nestbox was added to account for the box that they occupied.

Statistical Analysis

The data set only included nestlings that survived to fledging age (14 DPH). The model sets for natal recruitment included generalized Linear Models with a logit function (recruit yes/no). The model sets for natal dispersal distance (NDD) included generalized Linear Models with a gaussian function after the data were +1 log transformed. *A priori* hypotheses provided the framework for predictor selection. However, because sex was unknown for ~200 nestlings and because uneven sample sizes violate assumptions of Akaike's Information Criterion (AIC) modeling fitting (Burnham and Anderson, 2002), sex (and sex ratio of siblings) were excluded from models predicting recruitment and natal dispersal distance. Further, prior to running a preliminary global model, predictors were assessed for inter-collinearity. Two habitat quality factors, percent openness and distance to forest edge (m), were significantly positively correlated ($r = 0.59$, $p < 0.001$), thus distance to forest edge was omitted. No other predictor variables were strongly correlated. Next, I ran a preliminary global model for each dependent variable with predictors (egg laying date, year, body condition, natal territory openness, historical occupancy of the natal nestbox, and breeding year nestbox availability) and all possible interactions to determine significance of interaction terms. Interaction terms with $p > 0.2$ were not included in the global models. For recruitment, the only important interaction was between mass to tarsus ratio and percent openness of natal habitat (recruited ~ 1 + availability + openness + mass/tarsus + openness:mass/tarsus, $p = 0.033$). For NDD, the interactions between percent openness and year (log(NDD+1) ~ 1 + openness + year + openness:year; $p = 0.018$), and between mass to tarsus ratio and percent openness (log(NDD+1) ~ 1 + availability + openness + year + mass/tarsus + openness:mass/tarsus; $p = 0.098$), were both important and were included in the global model.

I used the dredge function in the MuMIn package in R version 4.2.1 to run the remaining possible combinations of predictors for data exploration with continuous predictors centered. I ranked individual models based on Akaike's Information Criterion for small sample sizes (AICc). I considered models to be biologically significant in predicting bluebird recruitment when ΔAICc ≤ 2.00 relative to the top model (Burnham and Anderson, 2002). I calculated parameter effect sizes for the top models using Jamovi v2.3. When predicting recruitment, because many top models potentially fit the data well, I model-averaged the beta estimates from this analysis (using the model.avg function in the MuMIn package in R 4.2.1) to determine which variables best explained the variance (Burnham and Anderson, 2002; Bolker et al., 2008; Bartoń, 2018).

Results

Overall Recruitment Rates and Natal Dispersal Distance

From 2019-2022, the number of breeding pairs of eastern bluebirds in the study population increased from 87, to 116, to 113, to 141 respectively. Capture rates of those adults was high and ranged from 82-98% for females and 69-88% for males (**Table 1**). Those birds produced 291 fledglings in 2019, 263 fledglings in 2020, and 268 fledglings in 2021. Of those, only 56 returned to the study site to breed (**Table 2**). The percentage of returning (banded) adults to naive (unbanded) adults tended to be higher for females (33-50%) than males (18-57%) and varied with year (**Table 3**).

Locally recruited bluebirds' natal dispersal distance (NDD) ranged from 0-20,466m (**Figure 5**). Average NDD was 5,419±6,700m. Of these, 14 recruited birds dispersed between MC and VC (ND > 10km) and were omitted to determine an average within-site ND distance (1739.79±1472.88m). This value (~1,740m) was used to represent the radius of the availability buffer used to determine available boxes within average natal dispersal range (**e.g., Figure 4**).

Predictors of Recruitment

A priori hypotheses based in eastern bluebird life history led to the prediction that local recruitment would be higher in males than females. Of the 822 birds that fledged from 2019-2021, sex was only known for 634. A binomial regression determined that sex was not a significant predictor of recruitment in the population ($R^2 = 0.003$, $p = 0.301$, $_{\text{residual}}\text{df} = 633$). Reduction in sample size and lack of significance between sex and recruitment, and sex and dispersal distance led to the exclusion of sex as a predictor variable in all future models.

Model exploration of recruitment via a global model through the dredge function yielded 7 models with ΔAICc ≤2 (**Table 4**). The top model, explaining 16% of the variation in the data set, showed a positive relationship between availability of nestboxes and recruitment (**Tables 4 and 5; Figure 6**). Model 2 (wt = 0.13) showed that recruitment is highest with high nestbox availability, and with varying combinations of mass to tarsus ratio and habitat openness (**Tables 4 and 5**). Lighter-weight birds (low mass/tarsus) were more likely to recruit when they fledged from a nestbox with less open habitat. Heavier birds (high mass/tarsus) were more likely to recruit from a nestbox with more open habitat (**Tables 4 and 5; Figure 7**). Model averaging was performed to determine average effects in all biologically significant models due to relative evenness in the top model's weights (**Table 6**). Overall, recruitment was best predicted by nestbox availability (relative importance (RI) = 0.96), followed by landscape openness (RI = 0.42), and then mass to tarsus ratio (RI = 0.37). However, there was a significant interaction between openness and mass to tarsus ratio on recruitment (RI = 0.28). Timing (early/late), historic bluebird occupancy and fledging year were all marginally important predictors of local recruitment (RI = 0.11, 0.10, 0.09 respectively; **Table 6**).

Predictors of Natal Dispersal Distance

Model exploration of predictors of dispersal distance based on a priori hypotheses (dredge function, MuMIn package, R) yielded 2 models with ΔAICc ≤2 (**Table 7**). The top model, explaining 41% of variation in the data, showed that decreased dispersal distance is associated with increased availability of nestboxes (**Table 8; Figure 8**) and decreased body size **(Table 8; Figure 9**). Natal dispersal distance was significantly shorter for birds fledged in 2021, compared to previous years (**Table 8; Figure 10**). Openness predicted dispersal distance, the extent of which was dependent on year; birds that fledged in 2019 and 2020 dispersed farther when fledged from more open habitats, while habitat openness did not predict NDD for birds fledged in 2021 (**Figure 10**). Model 2 explained only 16% of the variation and was identical to model 1 but excluded body condition (**Tables 7 and 8**).

Discussion

I found that recruitment and natal dispersal distance in eastern bluebirds are influenced jointly by intrinsic and extrinsic factors. Nesting location is clearly a resource that limits natal philopatry as bluebirds were more likely to recruit and dispersed shorter distances when there were more nestboxes available near their natal area during their first breeding season. Habitat quality also appears to influence philopatry, though not as expected. While I predicted a linear relationship between natal habitat openness and recruitment, I found an interaction between body condition and habitat openness such that fledglings that were heavier for their body size were more likely to recruit after fledging from territories with higher percentage of agricultural and grasslands. The opposite was true for fledglings that were lighter for their body size. Of the recruited birds, larger fledglings tended to have longer natal dispersal distance despite fledging from more open habitats. Birds that fledged from more open habitats dispersed farther in 2020 and 2021 (but not 2022). Though I predicted that males and birds that fledged later in the season were more likely to recruit to the natal population, sex and nest timing were not an important predictors of bluebird recruitment. Because the availability of nesting sites was the most important predictor of recruitment, these data suggest that competition is an important factor in settlement patterns. Body size at fledging, however, appears to benefit young birds in context-dependent ways. Overall, habitat availability, habitat quality, survival and competition likely shape natal philopatry in resident passerines.

This population of bluebirds displayed an overall recruitment rate of 6.8% (56/822) from 2020-2022. In general, local recruitment in this population of eastern bluebirds aligns with predicted values for resident passerine species, (median = 6.3%, range = 0-39%; Weatherhead and Forbes, 1994). In other populations of eastern bluebirds, recruitment likely varies with migration status, although data are limited. For example, in a Wisconsin population, recruitment varied yearly from 0.5-5% (Bauldry et al., 1995). Moreover, in non-migratory Southeastern breeding populations recruitment varied between 1-15% (Plissner and Gowaty, 1996; Lang, 2013). While year was not found to be a significant predictor of recruitment in the population, recruitment rate varied yearly from 5.3-7.6%. I found no significant relationship between fledgling sex and likelihood of recruitment or dispersal distances. Although the prediction that males would be more likely to recruit than females was based on overall trends and theory from passerine birds (Gowaty, 1993), data from eastern bluebirds is equivocal. Dispersal was greater for females than males in a South Carolina population studied in the 1980s (Plissner and Gowaty, 1996) but such a trend was not apparent in the same population 20 years later (Lang, 2013). Several studies have found evidence that natal philopatry is higher in presence of fewer opposite sex siblings (Cava et al., 2016), suggesting that another reason to disperse further could be to avoid competition with siblings or other kin (Eikenaar et al., 2007). Indeed, this mechanism appears to drive dispersal in the closely related western bluebird (*Sialia mexicana*; Aguillon and Duckworth, 2015) and would be a promising direction for future research in this population.

By far, habitat availability was the most important predictor of recruitment and dispersal distance; if more nestboxes were available in the breeding season post hatching, birds were more likely to recruit and dispersed shorter distances. These results make sense according to Waser (1985) who argues the competition drives dispersal such that animals should move to the first uncontested territory they encounter and no farther. Indeed, resources in the natal area can influence survival and kin behaviors (Brown and Brown, 1993). Sub-adult bluebirds likely spend late summer and autumn near their natal territory and thus may compete with kin for habitat. Life history theory predicts that competition between parents and offspring results in dispersal of offspring from natal territories. When breeding or food resources are limited, parents may be less tolerant of offspring remaining close to the natal territory and may displace them to avoid competition between kin (Bach et al., 2006). However, if nesting sites and food are abundant, kin tolerate offspring settling nearby (Aguillon and Duckworth, 2015).

Nestling body condition influenced both recruitment and dispersal distance in this population, suggesting that level of philopatry is influenced by intrinsic and extrinsic factors. While Jones et al. (2014) found that historic bluebird occupancy predicts the number of offspring fledged, I did not find that occupancy predicted natal philopatry. Land use, however, influenced both recruitment and dispersal distance, suggesting landscape composition has a more direct influence on levels of natal philopatry. The effect of body condition on recruitment was dependent on land use and this interaction is likely influenced by both competition with resident breeders and survival to the first breeding season. Smaller bluebirds were more likely to recruit when fledged from sites with low percent openness (closer to trees) and this could be explained by predation. Jackson et al. (2011) found that, soon after fledgling, bluebirds move into nearby forest edges and this likely protects them from predation by hawks. Thus, birds in poor body condition, because they should be poorer fliers, may need to be closer to forest edges to survive. Alternatively, larger bluebirds were more likely to recruit when fledged from sites with higher percent openness. Yet, larger fledglings also tended to disperse further and this may be explained better by competition than survival. Historic box occupancy data demonstrates that bluebirds prefer open habitats and fledge more young in these habitats (Jones et al., 2014). Tree swallows also prefer open habitats (Nelson, 2022), and often outcompete bluebirds for these territories (Jones et al., 2014). Therefore, although larger nestlings are more likely to recruit from these high-quality habitats, they may be outcompeted by more experienced birds and thus disperse farther.

A future direction for research would be to better understand the mechanisms that drive these habitat-morphological interactions. First, it would be good to understand the relative contributions of predation, foraging success and competition to natal philopatry. Second, quantification of habitat composition at fine-scale is needed. For example, in addition to measuring the distance from nestboxes to forest edges, it would be good to characterize edges of different sizes and compositions and distances to isolated trees. Moreover, assessment of grass height might influence natal dispersal or fitness as Ambardar et al. (2018) found that, although prey abundance is greater in tall grass, foraging success of bluebirds is greater in mowed grass. Finally, if competition is driving these natal philopatry patterns, it would be interesting to investigate whether similar morphological - habitat interactions exist among adult bluebirds.

Logistical limitations could have biased natal philopatry data; I captured and identified only the bluebirds breeding in nestboxes, but certainly some banded individuals moved to breed on privately owned land. This would cause a bias towards failing to recover the birds that disperse further. Of the recruited bluebirds, five were observed breeding for the first time 2 years post hatch, and two were first observed breeding 3 years post hatch. Having missed these birds' first broods, and because 14 of 56 (25%) birds were recovered >20 km from their natal territory, I assume that some dispersed birds were missed. Also, adult capture rates demonstrate a consistent rate of capture in that ~88% of breeding birds are captured each year. However, males are captured at a 14% lower rate than females. Reduced capture rate of males would under-estimate male recruitment and thus I might have missed weak but important sex biases in recruitment. Future approaches could employ citizen science programs and re-sight locally recruited bluebirds outside of the study area which would increase the reliability of the recruitment parameters.

This study emphasizes the importance of considering both intrinsic and extrinsic factors when studying recruitment in a resident songbird. Natal philopatry is a complex product of post-fledging survival, propensity to disperse and competition for nesting sites. Naturally, the most limiting factor of recruitment in this population is availability of nestboxes. Indeed, it has been suggested that cavity-nesting species are limited by availability of cavities rather than food when acquiring territories (Miller, 2010). Nonetheless, I also found that interactions between body condition and habitat quality influenced recruitment, highlighting the importance of assessing a multitude of variables when predicting avian recruitment.

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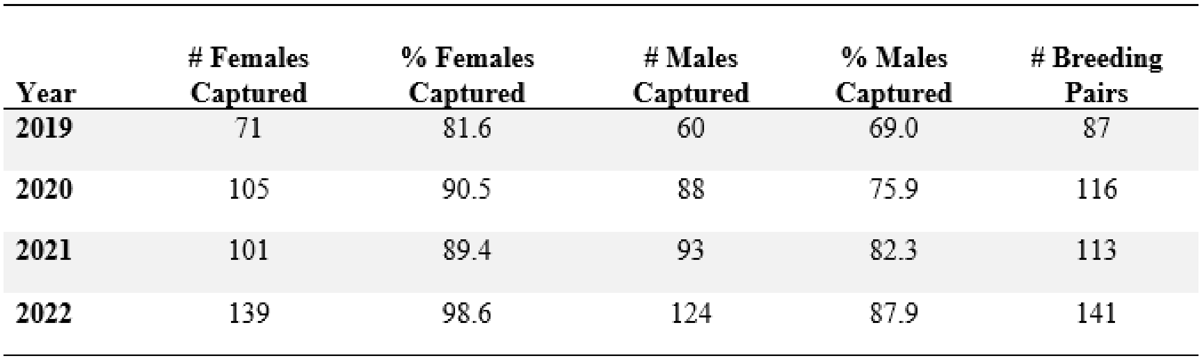
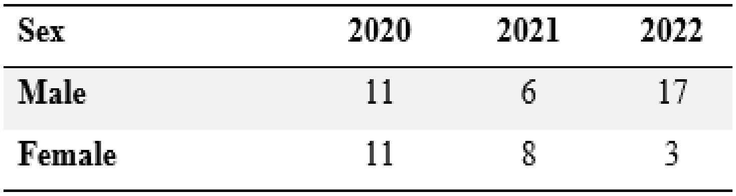
Appendix

Table 1. The total number of adult eastern bluebirds breeding at nestboxes, and the number and percent that were captured and banded by year.



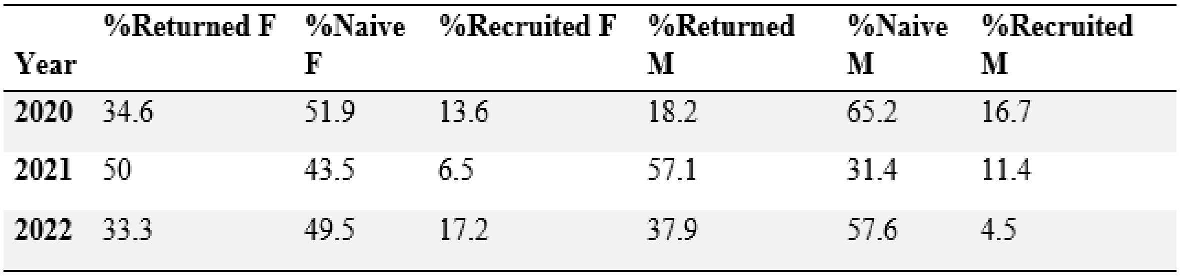
Year	# Females Captured	% Females Captured	# Males Captured	% Males Captured	# Breeding Pairs
2019	71	81.6	60	69.0	87
2020	105	90.5	88	75.9	116
2021	101	89.4	93	82.3	113
2022	139	98.6	124	87.9	141

Table 2. Number of eastern bluebirds recruited into the local population that were banded as nestlings in a prior year at the Watauga County, NC field site.



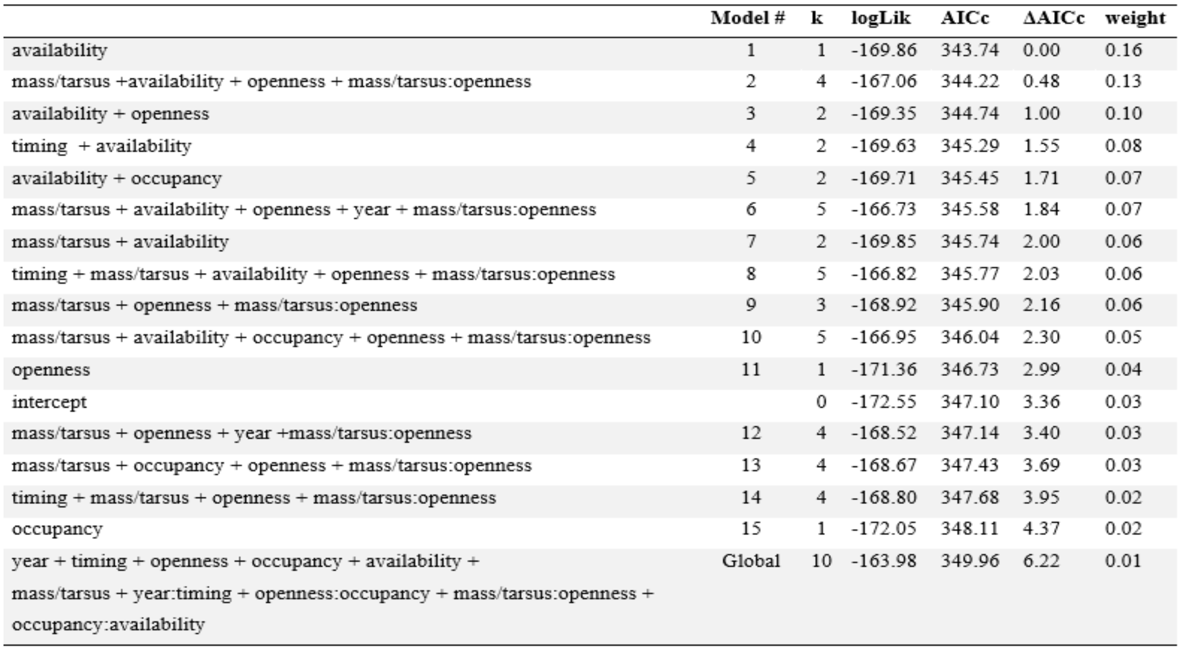
Sex	2020	2021	2022
Male	11	6	17
Female	11	8	3

Table 3. The percent of adult eastern bluebirds breeding at nestboxes at the Watauga County, NC field site. The percent of breeding birds that were previously banded as adults (returned female and male), those that were captured that had not been previously banded (naive) and adults that were banded as nestlings (recruited), data split by year.



Year	%Returned F	%Naive F	%Recruited F	%Returned M	%Naive M	%Recruited M
2020	34.6	51.9	13.6	18.2	65.2	16.7
2021	50	43.5	6.5	57.1	31.4	11.4
2022	33.3	49.5	17.2	37.9	57.6	4.5

Table 4. Model comparison of top 15 generalized linear models (logit link, centered cont. variables) predicting local recruitment in a population of eastern bluebirds in Watauga County, NC. Availability = number of available nestboxes in a 1,740m radius buffer around a bird's natal nestbox during its second year. Interaction terms are indicated by ":". Mass/tarsus = ratio mass (g) to the length of the tibiotarsus (mm) at 14 DPH. Openness = summation of the percent cropland and percent rangeland of a bird's natal feeding territory (100m radius buffer). Occupancy = % of total available years in which a bluebird nested in the natal box. Timing = binomial, nests with first egg laid before or after May 25th (0 = before, 1 = after). Year = birds hatch year. K = number of parameters, logLik = log(likelihood). Weight = relative weight of variation explained by each model.

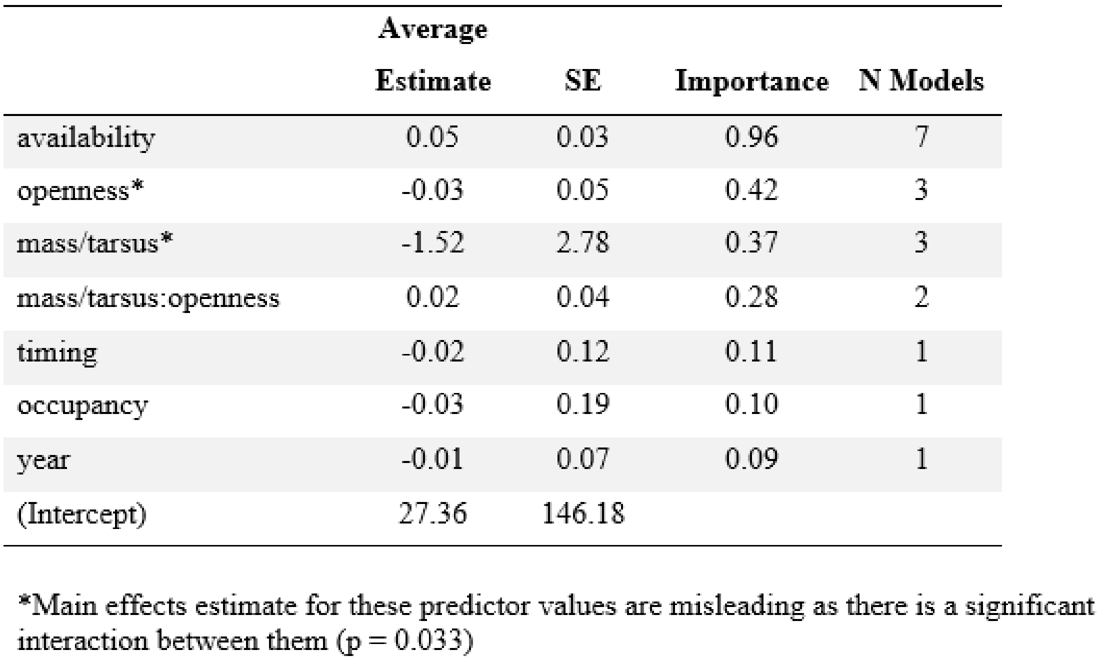


	Model #	k	logLik	AICc	ΔAICc	weight
availability	1	1	-169.86	343.74	0.00	0.16
mass/tarsus +availability + openness + mass/tarsus:openness	2	4	-167.06	344.22	0.48	0.13
availability + openness	3	2	-169.35	344.74	1.00	0.10
timing + availability	4	2	-169.63	345.29	1.55	0.08
availability + occupancy	5	2	-169.71	345.45	1.71	0.07
mass/tarsus + availability + openness + year + mass/tarsus:openness	6	5	-166.73	345.58	1.84	0.07
mass/tarsus + availability	7	2	-169.85	345.74	2.00	0.06
timing + mass/tarsus + availability + openness + mass/tarsus:openness	8	5	-166.82	345.77	2.03	0.06
mass/tarsus + openness + mass/tarsus:openness	9	3	-168.92	345.90	2.16	0.06
mass/tarsus + availability + occupancy + openness + mass/tarsus:openness	10	5	-166.95	346.04	2.30	0.05
openness	11	1	-171.36	346.73	2.99	0.04
intercept		0	-172.55	347.10	3.36	0.03
mass/tarsus + openness + year +mass/tarsus:openness	12	4	-168.52	347.14	3.40	0.03
mass/tarsus + occupancy + openness + mass/tarsus:openness	13	4	-168.67	347.43	3.69	0.03
timing + mass/tarsus + openness + mass/tarsus:openness	14	4	-168.80	347.68	3.95	0.02
occupancy	15	1	-172.05	348.11	4.37	0.02
year + timing + openness + occupancy + availability + mass/tarsus + year:timing + openness:occupancy + mass/tarsus:openness + occupancy:availability	Global	10	-163.98	349.96	6.22	0.01

Table 5. Odds ratios of biologically significant models predicting eastern bluebird recruitment at the Watauga County, NC field site. See Table 4 Legend for variable descriptions.

	Predictor	Effect	Odds Ratio	Lower 95% CI	Upper 95% CI
Model 1	(Intercept)	-	0.0734	0.0530	0.0986
	Availability	+	1.0534	1.0079	1.1040
Model 2	(Intercept)	-	0.0685	0.0483	0.0935
	Availability	+	1.0462	0.9993	1.0987
	Openness	+	1.0057	0.9957	1.0164
	Mass/Tarsus	-	0.5373	0.0433	6.8885
	Openness: Mass/Tarsus		1.0853	1.0068	1.1660
Model 3	(Intercept)	-	0.0728	0.0524	0.0979
	Openness	+	1.0050	0.9954	1.0151
	Availability	+	1.0471	1.0010	1.0986
Model 4	(Intercept)	-	0.0731	0.0527	0.0982
	Timing (late – early)	-	0.8089	0.4316	1.4758
	Availability	+	1.0550	1.0091	1.1060
Model 5	(Intercept)	-	0.0732	0.0528	0.0984
	Availability	+	1.0510	1.0046	1.1022
	Occupancy	-	0.7419	0.2579	2.1493
Model 6	(Intercept)	-	0.0678	0.0476	0.0928
	Mass/Tarsus	-	0.4627	0.0360	6.1033
	Availability	+	1.0456	0.9986	1.0983
	Openness	+	1.0059	0.9956	1.0167
	Year	-	0.8598	0.5961	1.2326
	Openness: Mass/Tarsus		1.0900	1.0095	1.1736

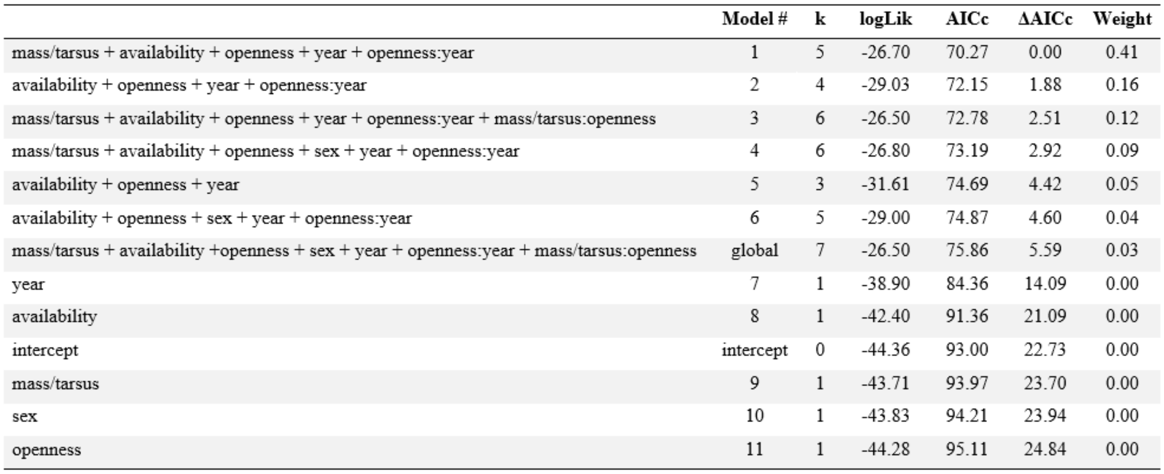
Table 6. Model averaged effect sizes (“Estimate”) of all biologically significant predictors (in GLM with ΔAICc ≤2) of local recruitment in a population of eastern bluebirds at the Watauga County, NC fieldsite. See Table 4 legend for predictor descriptions, “Importance” = sum of model weights (sw) over all models including predictor, N Models = number of models ΔAICc ≤2 predictor variables are in.



	Average Estimate	**SE**	**Importance**	**N Models**
availability	0.05	0.03	0.96	7
openness*	-0.03	0.05	0.42	3
mass/tarsus*	-1.52	2.78	0.37	3
mass/tarsus:openness	0.02	0.04	0.28	2
timing	-0.02	0.12	0.11	1
occupancy	-0.03	0.19	0.10	1
year	-0.01	0.07	0.09	1
(Intercept)	27.36	146.18		

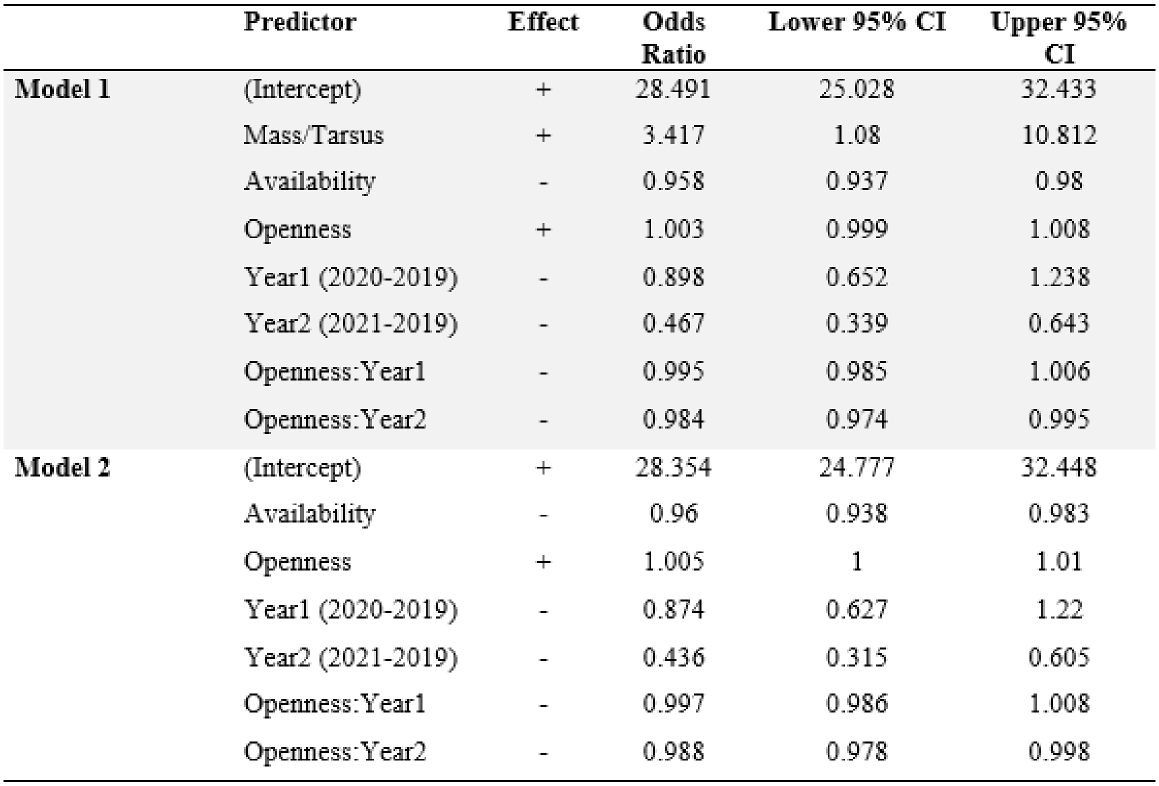
*Main effects estimate for these predictor values are misleading as there is a significant interaction between them (p = 0.033)

Table 7. Generalized linear models (identity link, gaussian dependent, centered cont. variables) AICc comparison predicting log (natal dispersal distance (m)+1) in eastern bluebirds at the Watauga County, NC fieldsite. See Table 4 legend for variable descriptions.



	Model #	k	logLik	AICc	ΔAICc	Weight
mass/tarsus + availability + openness + year + openness:year	1	5	-26.70	70.27	0.00	0.41
availability + openness + year + openness:year	2	4	-29.03	72.15	1.88	0.16
mass/tarsus + availability + openness + year + openness:year + mass/tarsus:openness	3	6	-26.50	72.78	2.51	0.12
mass/tarsus + availability + openness + sex + year + openness:year	4	6	-26.80	73.19	2.92	0.09
availability + openness + year	5	3	-31.61	74.69	4.42	0.05
availability + openness + sex + year + openness:year	6	5	-29.00	74.87	4.60	0.04
mass/tarsus + availability +openness + sex + year + openness:year + mass/tarsus:openness	global	7	-26.50	75.86	5.59	0.03
year	7	1	-38.90	84.36	14.09	0.00
availability	8	1	-42.40	91.36	21.09	0.00
intercept	intercept	0	-44.36	93.00	22.73	0.00
mass/tarsus	9	1	-43.71	93.97	23.70	0.00
sex	10	1	-43.83	94.21	23.94	0.00
openness	11	1	-44.28	95.11	24.84	0.00

Table 8. Odds ratios of top 2 generalized linear models (identity link) predicting eastern bluebird natal dispersal distance (+1, log transformed) at the Watauga County, NC fieldsite. See Table 4 legend for predictor descriptions.



	Predictor	Effect	Odds Ratio	Lower 95% CI	Upper 95% CI
Model 1	(Intercept)	+	28.491	25.028	32.433
	Mass/Tarsus	+	3.417	1.08	10.812
	Availability	-	0.958	0.937	0.98
	Openness	+	1.003	0.999	1.008
	Year1 (2020-2019)	-	0.898	0.652	1.238
	Year2 (2021-2019)	-	0.467	0.339	0.643
	Openness:Year1	-	0.995	0.985	1.006
	Openness:Year2	-	0.984	0.974	0.995
Model 2	(Intercept)	+	28.354	24.777	32.448
	Availability	-	0.96	0.938	0.983
	Openness	+	1.005	1	1.01
	Year1 (2020-2019)	-	0.874	0.627	1.22
	Year2 (2021-2019)	-	0.436	0.315	0.605
	Openness:Year1	-	0.997	0.986	1.008
	Openness:Year2	-	0.988	0.978	0.998

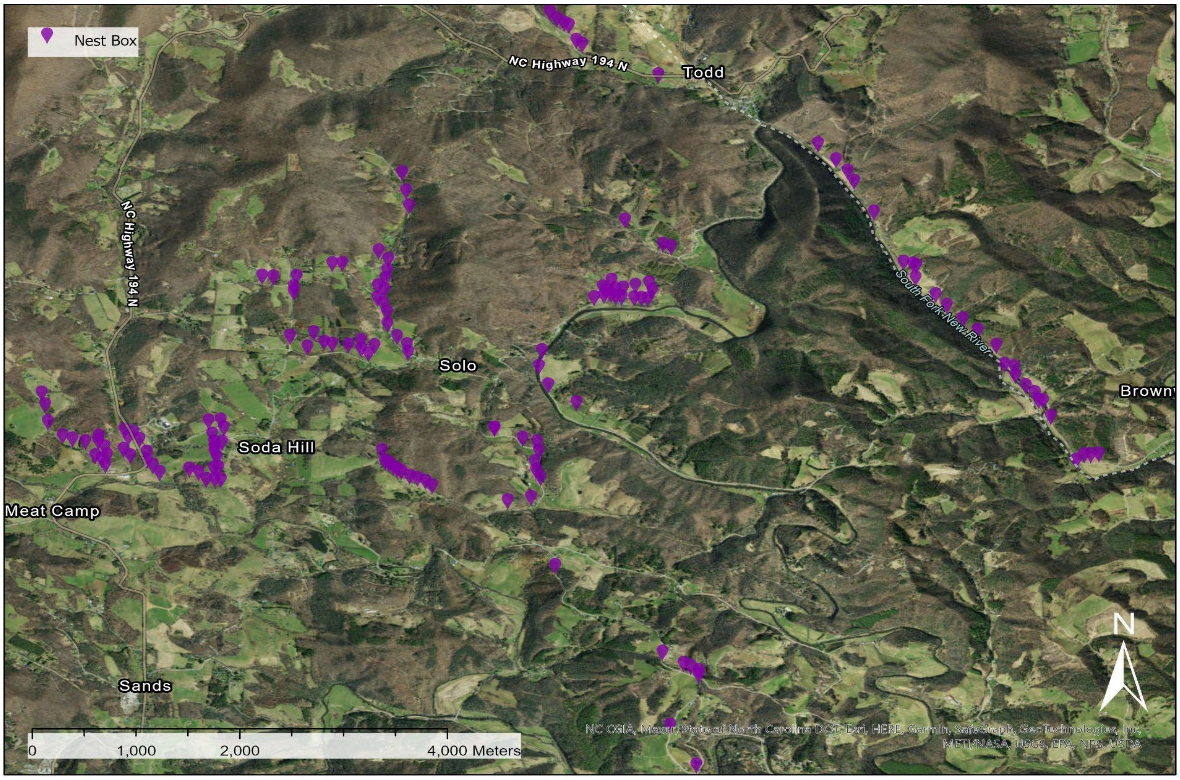


Figure 1. Hybrid map of wooden nestboxes near Meat Camp, NC, USA. Violet pins indicate the location of a wooden nestbox. Created using ArcGIS Pro® software by Esri.

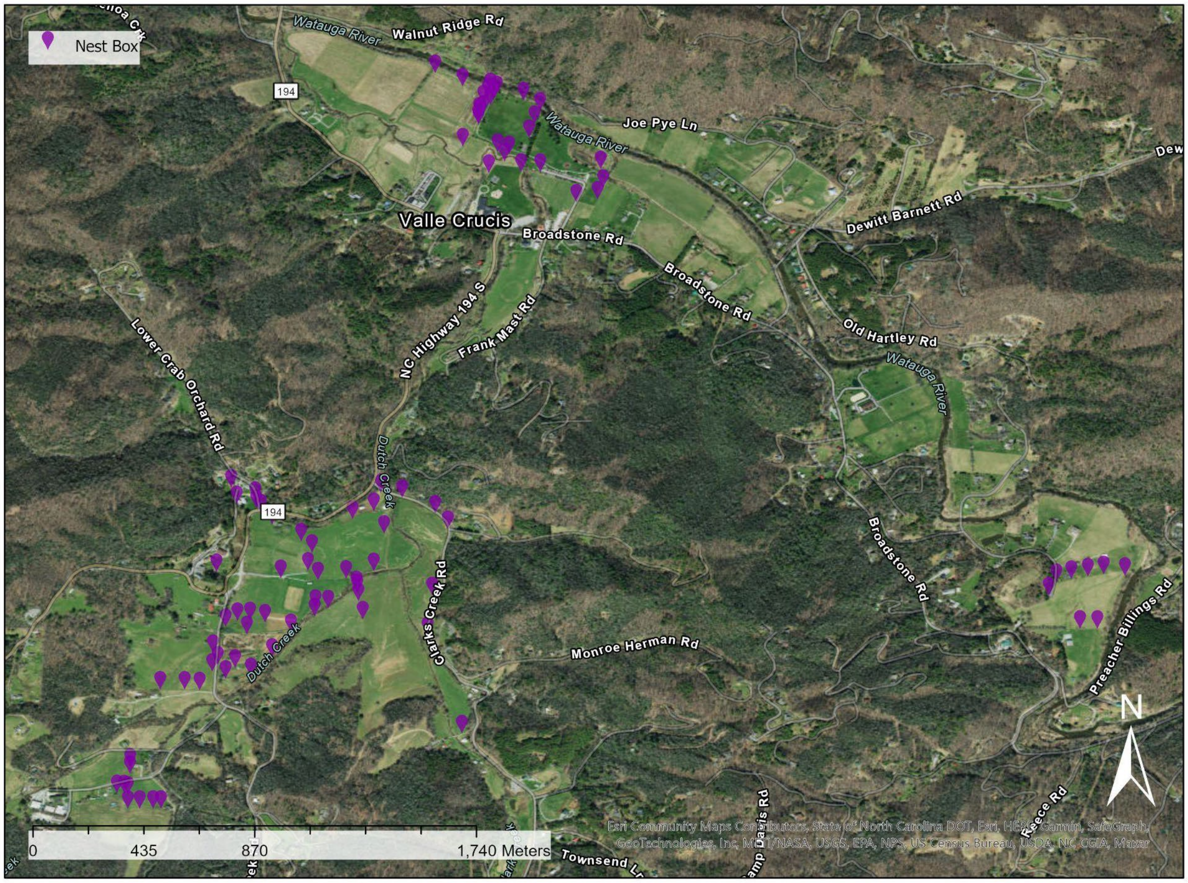


Figure 2. Hybrid map of wooden nestboxes near Valle Crucis, NC, USA. Violet pins indicate the location of a wooden nestbox. Created using ArcGIS Pro® software by Esri.

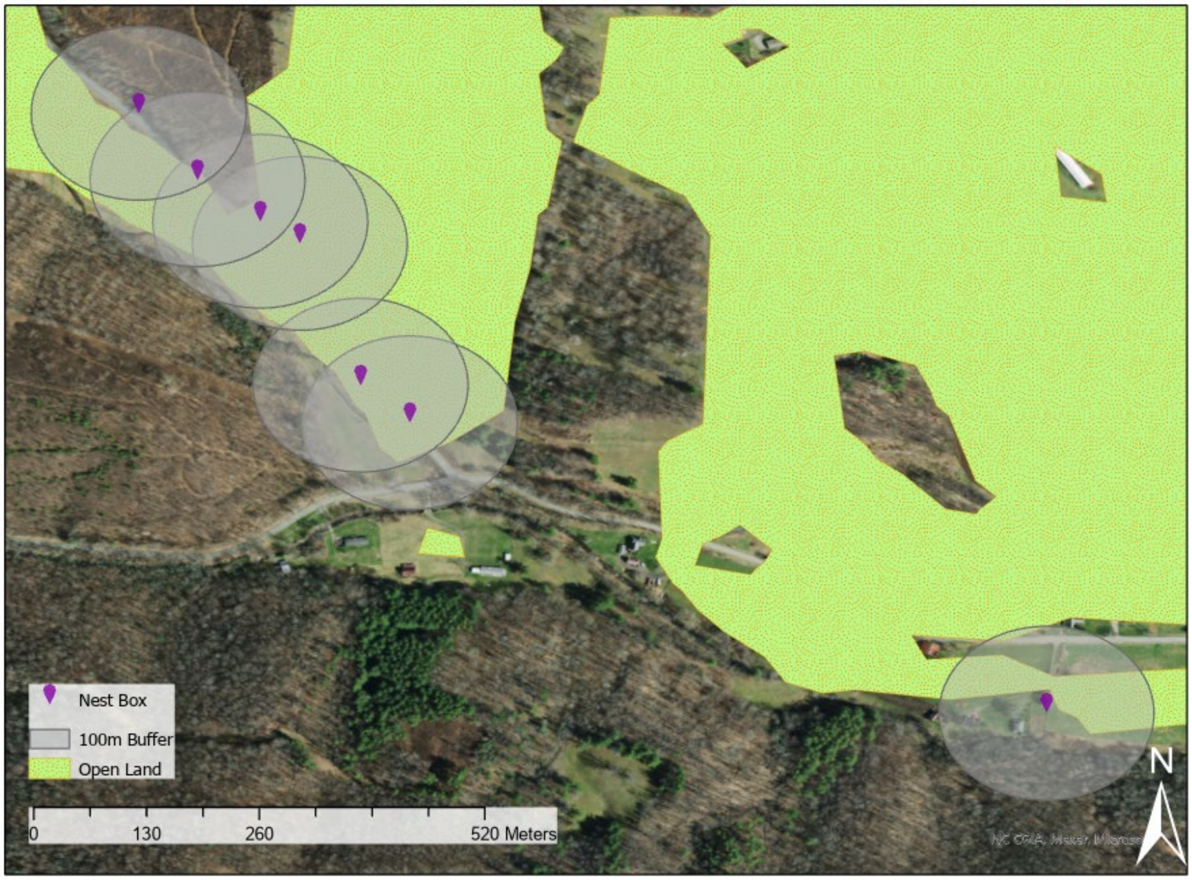


Figure 3. An example of the 100m radius territory buffers (gray) used to calculate natal habitat openness. Violet pins represent a nestbox. Lime green polygons with orange speckle represents "open" land, classified as rangeland or crops by Sentinel-2 10m Land Use/Land Cover Time Series (Mature Support), Esri, 2022. Created using ArcGIS Pro® software by Esri.

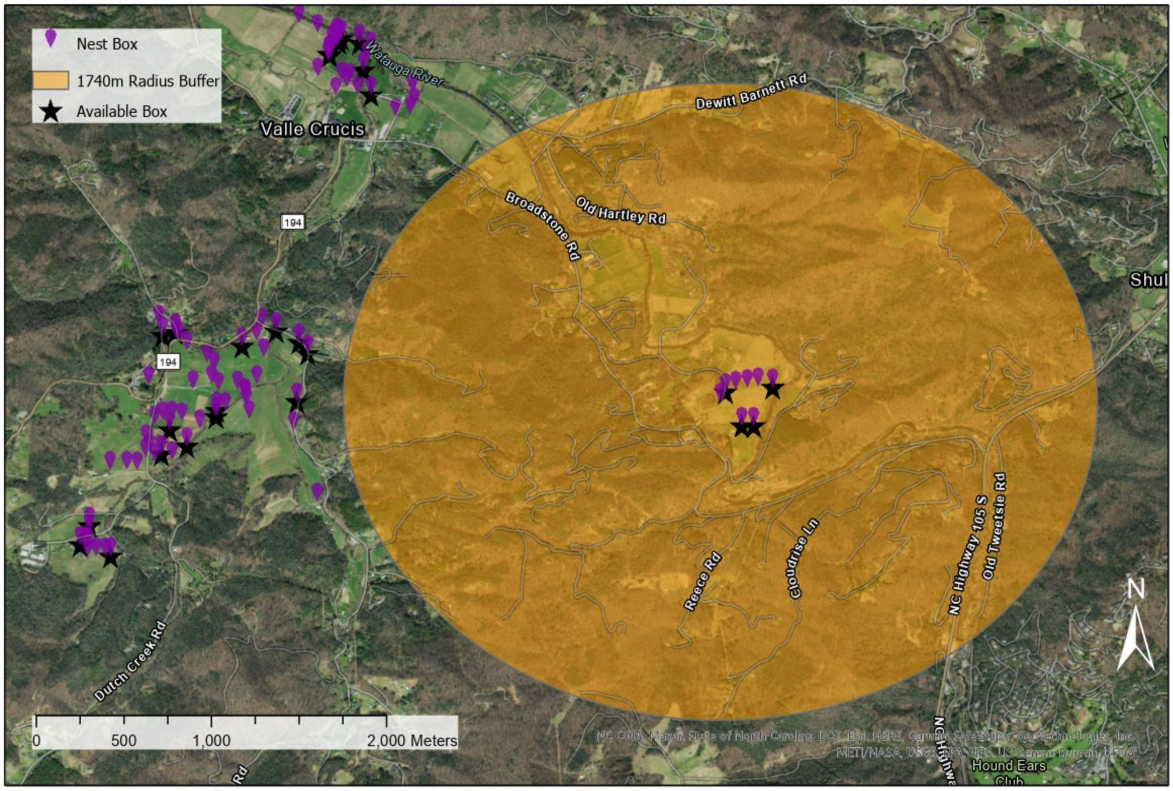
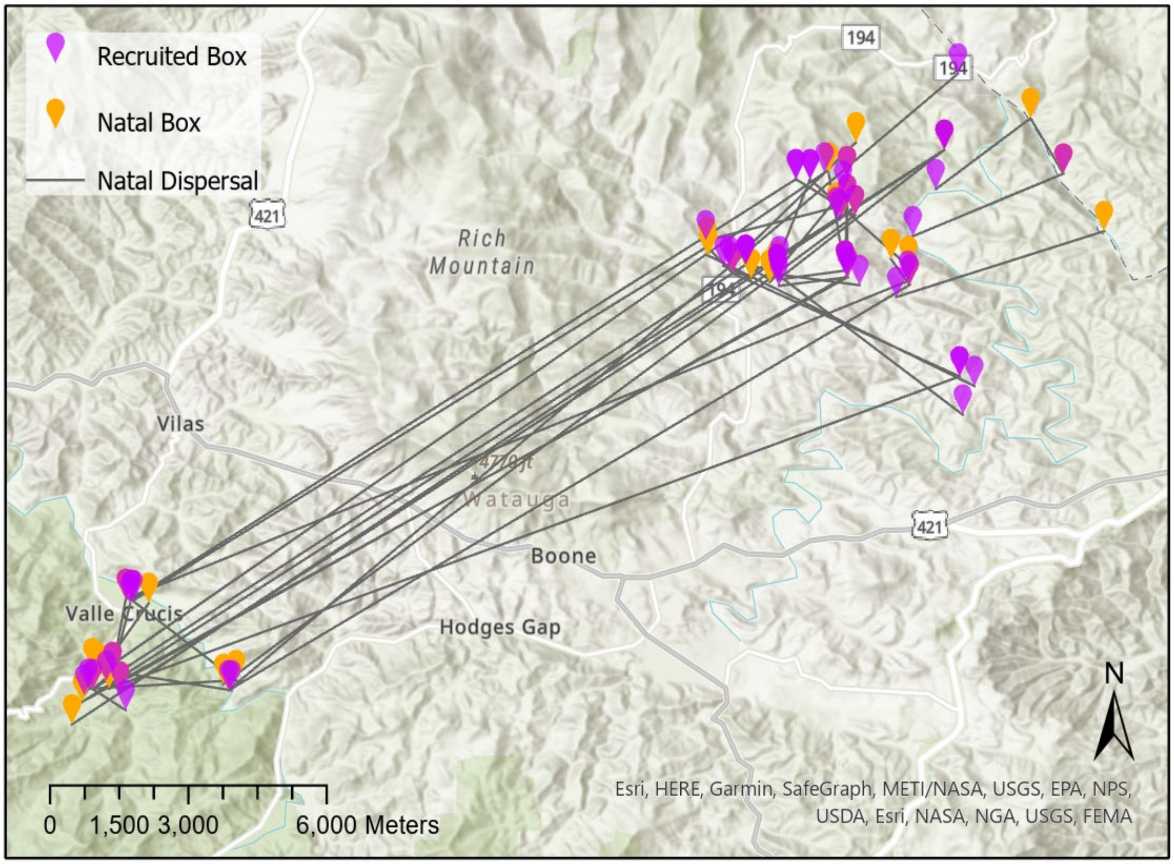


Figure 4. An example of the buffer used to survey availability of boxes surrounding natal nest site. The buffer (orange) is 1,740m radius or the average dispersal distance in an isolated site (Valle Crucis). Violet pins indicate a nestbox, pins with a black star beneath indicate an available nestbox. Created using ArcGIS Pro® software by Esri.



Esri, HERE, Garmin, SafeGraph, METI/NASA, USGS, EPA, NPS, USDA, Esri, NASA, NGA, USGS, FEMA

Figure 5. Natal dispersal patterns of eastern bluebirds across two spatially segregated field sites in Watauga County, NC. Orange pins represent the box a bluebird fledged from (“Natal Box”), violet pins represent the box a bluebird raised its first clutch in (“Recruited Box”. Charcoal gray lines represent linear distance from the natal box to the recruited box. Created using ArcGIS Pro® software by Esri.

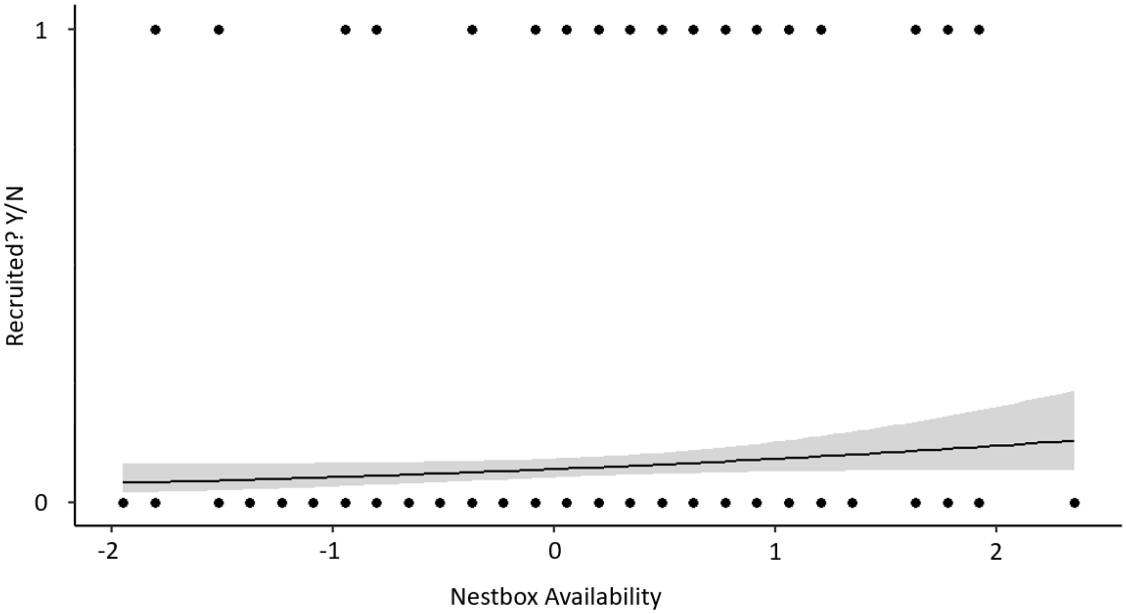


Figure 6. Effect of nestbox availability within a 1,740m (average natal dispersal distance) radius surrounding the natal nests on eastern bluebird recruitment in Watauga Co. NC. Availability is z-standardized. 0 = not recruited, 1 = recruited. Shaded bands represent 95% confidence interval of the predicted relationship.

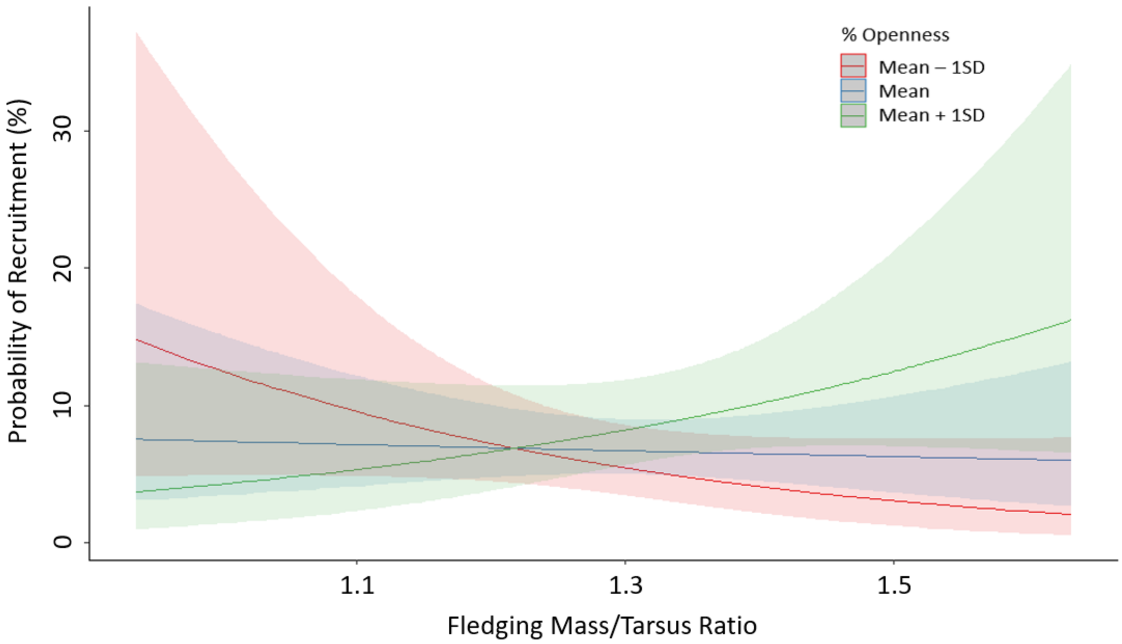


Figure 7. Effect of mass (g) to tarsus (mm) ratio at fledging on probability of local recruitment (generalized linear model, logit link) of eastern bluebirds with respect to natal territory openness (summative percent cropland or rangeland). Openness is categorized as +1 standard deviation from the mean, mean and -1 standard deviation of the mean. Shaded bands represent 95% confidence interval of the predicted relationship.

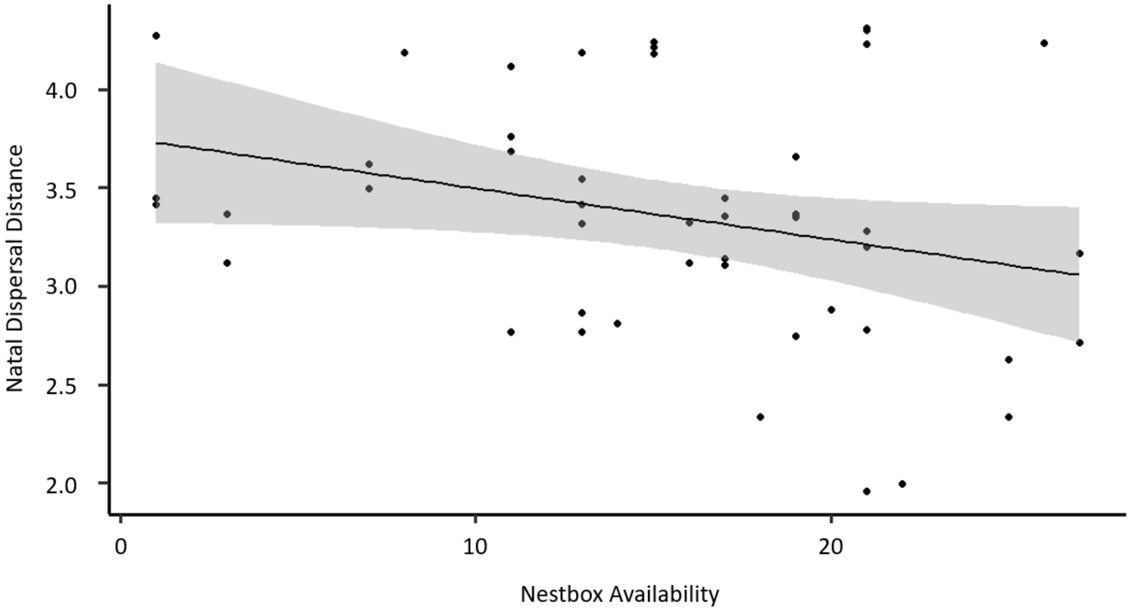


Figure 8. Relationship between nestbox availability and natal dispersal distance (+1 log transformed) for recruited eastern bluebirds in Watauga Co., NC. Shaded bands represent 95% confidence interval of the predicted relationship.

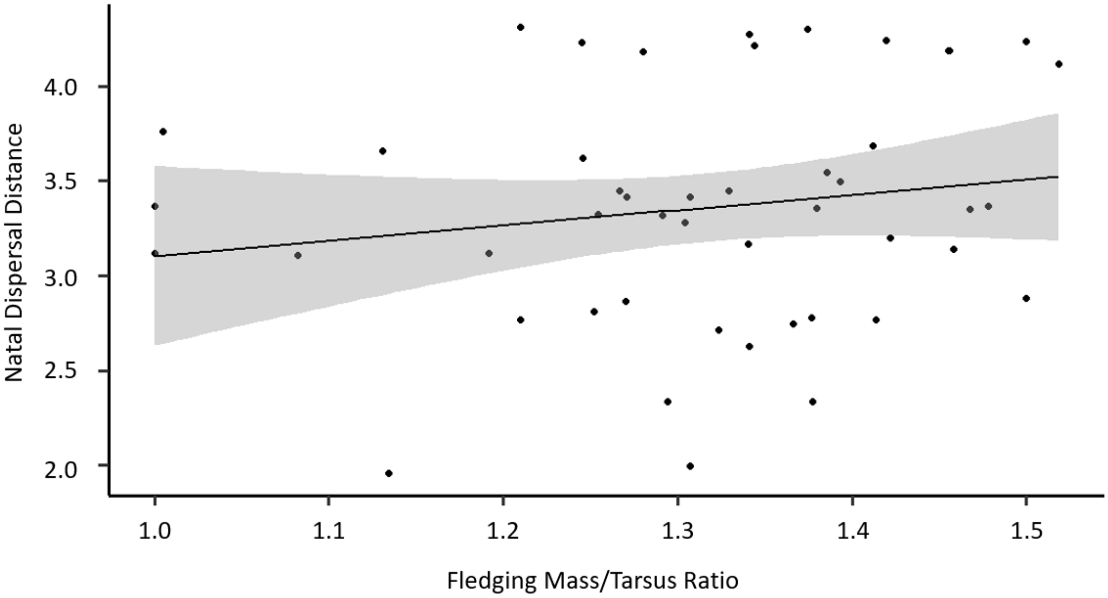


Figure 9. Relationship between mass (g) to tarsus (mm) ratio at fledging and dispersal distance (m; +1 log transformed) for recruited eastern bluebirds in Watauga Co., NC. Shaded bands represent 95% confidence interval of the predicted relationship.

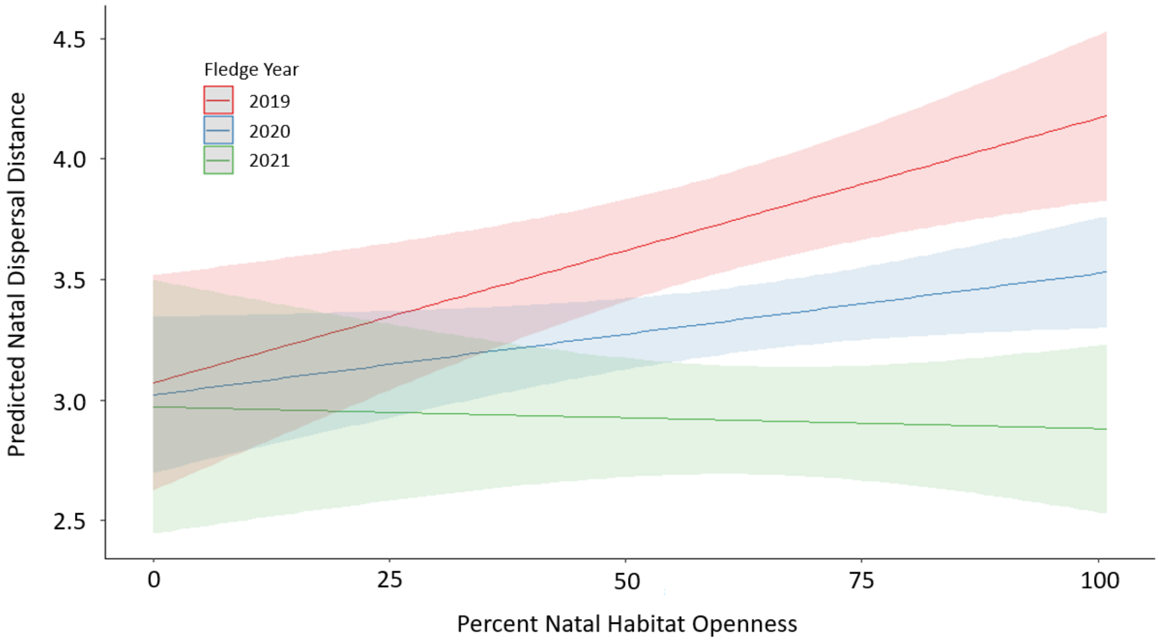


Figure 10. Effect of natal habitat openness (% rangeland or crops with a 100m radius surrounding the natal nest) on predicted natal dispersal distance (m; NDD; generalized linear model, identity link, NDD +1 log transformed). Data are separated by hatch year (2019, 2020, 2021). Shaded bands represent 95% confidence interval of the predicted relationship.

Vita

Sarah D. Hill was born in Frederick, Maryland in 1996. She attended primary school in Frederick County, MD. She enrolled in classes at the University of North Carolina at Wilmington in the fall of 2014, and graduated with her Bachelor of Science degree in Biology in 2018. In the fall of 2019, she began her Master’s research studying disease ecology and avian behavior under the supervision of Dr. Lynn Siefferman. In the spring of 2022, due to complications beyond her control, Sarah was unable to continue her intended study and began a new Master’s project. She completed her Master’s research on recruitment and natal dispersal in the Eastern Bluebird and received her Master of Science degree in Ecology, Evolution and Environmental Biology in December 2022.