FRIEND OR FOE? THE INFLUENCE OF NEIGHBOURS ON REPRODUCTIVE
SUCCESS OF MOUNTAIN BLUEBIRDS AND TREE SWALLOWS

by

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ABSTRACT

During the breeding season, secondary cavity nesting birds are often limited by the availability of suitable nesting locations. The placement of artificial nest boxes on the landscape not only provides potential nesting sites, but it can also lead to interactions within and between species. This thesis examines the influence of conspecific and heterospecific neighbours on the reproductive success of mountain bluebirds (*Sialia currucoides*) and tree swallows (*Tachycineta bicolor*) and the occurrence of extra-pair offspring at mountain bluebird nests. Increased tree swallow neighbour abundance early in the season negatively influenced the hatching success of mountain bluebirds. However, an increase in tree swallow neighbour abundance had a positive influence on the fledging success of tree swallows and mountains bluebird later in the season. While improved fledging success with increased tree swallow neighbour abundance may be due to shared nest defense or habitat quality, repeated interruption of incubating female bluebirds by tree swallow neighbours may put eggs at risk and reduce hatching success. Together, these results indicate that the influence of conspecific and heterospecific neighbours on reproductive success varies by species and phase of reproduction.

The abundance of conspecific neighbours also influences extra-pair paternity in mountain bluebirds. The occurrence of extra-pair nestlings at bluebird nests increased as neighbour abundance within 500m and 1000m increased. In contrast, we detected a decrease in the occurrence of extra-pair offspring in bluebird nests as the abundance of conspecific neighbours increased within 250m of the nest. Although an increase in neighbour abundance increases the opportunity of extra-pair copulations, more neighbours relatively close by likely increases mate-guarding to mitigate extra-pair copulations. Indeed, bluebirds in our study travel an average of over 2000m in search of extra-pair mates. These findings are consistent with other studies of increasing neighbour densities leading to increased extra-pair mating opportunities and increased mate-guarding activity to reduce paternity loss.

Together, these results highlight the importance of exploring conspecific and heterospecific neighbour interactions throughout the nesting period. Future behavioural and tracking studies may provide insight into the mechanisms that produce variation in mountain

bluebird and tree swallow reproductive success and strategies employed by both male and female bluebirds when seeking extra-pair copulations.

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ACKNOWLEDGEMENTS

DEDICATION

From the time I was a child I have been fascinated by birds. While I have always received tremendous support from all of my family, my maternal grandmother, Waltraut "Trudy" Trulsen, not only supported my love of birds, but she also encouraged me to pursue higher education. I dedicate this thesis to you, grandma.

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CHAPTER 1: INTRODUCTION

Whether for food, protection from pests, or companionship, humans have been providing birds with artificial nesting sites for centuries (Froke 1983). By the mid-twentieth century in North America, landowners, having noticed declines in secondary cavity nesting birds like bluebirds and tree swallows, began erecting nest boxes (Froke 1983). Secondary cavity nesting birds are particularly susceptible to habitat loss as they are often limited by the availability of suitable nest sites (Martin 2015) and nest boxes provide a critical resource in areas altered for human use (e.g., agriculture, forestry) or by climate change. Concern over the decline of eastern bluebirds (*Sialia sialis*) in the United States, led to the development of large-scale nest box deployment and monitoring programs through the establishment of bluebird trails (Kibler 1969; Froke 1983). These bluebird trail monitoring programs provide not only nesting locations, but they also provide an opportunity for research into the reproductive behaviours and interactions of secondary cavity nesting birds (Froke 1983; Møller 1992; Mänd et al. 2005; McArthur et al. 2017).

Along bluebird trail monitoring routes, some nest boxes are placed close together. While this approach can result in high population densities, reproductive interference can result from aggressive interactions between neighbours as individuals establish territories and defend resources (Hinde 1956; Tumulty et al. 2018; Jiang et al. 2022; Lipshutz and Rosvall 2021). Interference from conspecific neighbours can have negative effects on reproductive success due to territory loss and thus reduced resource availability (Andren 1990; Dunn et al. 2021). Neighbour interactions can also cause individuals to be distracted from incubation, causing additional negative consequences (Gröning and Hochkirch 2008; Deeming et al. 2017; Croston et al. 2021). It is not uncommon, however, for the frequency of aggressive interactions between neighbours to decline over time as individuals become familiar with one another (Tumulty et al. 2018; Humphries et al. 2021). This diminished aggression toward familiar neighbours is referred to as the "dear enemy" effect (Fisher 1954). By reducing aggression toward established neighbours, individuals can save time and energy otherwise spent on territorial defence (Tumulty 2022; Jin et al. 2022).

While there can be negative consequences, some interactions with neighbours can also be beneficial through improved reproductive success (Krams et al. 2008) by mobbing and byproduct nest defence (Ligon 1983; Russel and Wright 2009), or information transfer (Brow 1988; Campobello and Hare 2007).

Nesting near heterospecific neighbours may provide early detection of threats by eavesdropping on alarm calls (Turner et al. 2023; Zhou et al 2024). The ability to recognize the alarm calls of heterospecific and conspecific neighbours may improve reproductive success (Magrath et al. 2015; Szymkowiak 2022).

The influence of neighbours not only affects reproductive success but can also impact extra-pair paternity. Greater than 80% of songbird species studied are socially rather than genetically monogamous: both male and female help to rear the offspring but also seek extra-pair copulations as part of a mixed mating strategy (Brouwer and Griffith 2019). Male songbirds benefit from engaging in extra-pair copulations directly through increased reproductive success (Webster et al. 1995); however, they do so at the risk of conflict with neighbouring territory owners and paternity loss at their own nest (Westeneat and Stewart 2003). Females typically seek extra-pair copulations to acquire genetic, resource, and fertility insurance benefits (Gray 1997; Griffith et al. 2002; Forstmeier et al. 2014). The pursuit of extra-pair copulations by females is also not without its risks. Females engaging in extra-pair copulations that are "caught" by their within-pair mate may experience physical retaliation (Valera et al. 2003) whereas females that do not engage in extra-pair copulations may receive more help from their within-pair male (Matysioková and Remeš 2013). The frequency of extra-pair paternity varies widely among songbirds, with some species having no extra-pair offspring, while have greater than 80% of nestlings sired by extra-pair males (Birkhead and Møller 1995; Wang et al. 2021; Dunning et al. 2023).

Studies of the causes and consequences of extra-pair paternity often focus on sexually selected traits (Whittingham and Dunn 2016; Benitez Saldivar et al. 2022; Thibault et al 2022; Valcu et al. 2023); however, variation in extra-pair paternity can also be associated with neighbour abundance (Birkhead et al. 1992; Brown and Brown 1996; Mayer and Pasinelli 2013). Opportunities for extra-pair copulations increase as the availability of potential mates increases. In some songbirds, the frequency of extra-pair paternity is

positively associated with neighbour density (Birkhead et al. 1992; Krokene and Lifield 2000; Rowe and Weatherhead 2007). However, as neighbour density increases, mate guarding (Kokko and Morrell 2005; Akcay et al. 2009) and territory defense also increase (Barrero et al. 2023) and while these behaviours help to mitigate loss of paternity at the nest, they can also reduce the opportunity for males to engage in extra-pair copulation (Hasselquist and Bensch 1991).

My research investigates how conspecific and heterospecific neighbour abundance and proximity impacts the reproductive success of mountain bluebirds (*Sialia currucoides*) and tree swallows (*Tachycineta bicolor*); it also looks at patterns of extra-pair paternity in mountain bluebirds in southern British Columbia. Mountain bluebirds and tree swallows are migratory songbirds that inhabit large open spaces adjacent to wooded areas. Both species are secondary cavity-nesters who frequently use nest boxes. As such, they can find themselves in direct competition for nest sites where their ranges overlap in western North America.

To examine the influence of neighbours on reproductive success (Chapter 2), I used data on nest box activity collected by volunteers of the Kamloops Naturalist Club's Bluebird Trails Monitoring Program along routes in and around Kamloops, British Columbia. I created a distance matrix (Appendix Figure A.1) of all active nest boxes to ask how conspecific and heterospecific neighbours influence reproductive success during early (hatching success) and late stages (fledging success) of nesting. In chapter three, I describe how I collected DNA samples from adults and nestling mountain bluebirds for paternity assignment and ask how the distance and proximity of conspecific and heterospecific neighbours influence patterns of extra-pair paternity.

The addition of nestboxes on the landscape provides secondary cavity nesting birds with an important and potentially scarce resource and has been crucial for the recovery and persistence of bluebirds and tree swallows in many parts of their range. The goal of this research is to provide a better understanding of how the proximity and abundance of both conspecific and heterospecific neighbours impacts reproductive success and extra-pair paternity. Information gained from this research can help guide effective placement of nest

boxes in terms of abundance and spacing and ultimately inform effective management by both professionals and community science organizations.

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CHAPTER 2: THE INFLUENCE OF CONSPECIFIC AND HETEROSPECIFIC NEIGHBOURS ON AVIAN REPRODUCTIVE SUCCESS.

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ABSTRACT

We investigated the influence of conspecific and heterospecific neighbours on the reproductive success of mountain bluebirds (*Sialia currucoides*) and tree swallows (*Tachycineta bicolor*) over eight breeding seasons. The abundance of heterospecific neighbours was negatively associated with reproductive success in mountain bluebirds but positively associated with reproductive success in tree swallows during the early nesting period (i.e., hatching success). For bluebirds, conspecific and heterospecific neighbour abundance was associated with higher reproductive success (i.e., fledging rate) during the later stages of the nesting period; the same was true for conspecific abundance for tree swallows. These findings could be explained by either positive behavioural interactions (e.g., shared defence) or by habitat quality. We found contrasting effects of nearest neighbour distance. For both mountain bluebirds and tree swallows, having a tree swallow neighbour in close proximity was positively associated with reproductive success during the early nesting period, while having a mountain bluebird neighbour in close proximity was negatively associated with reproductive success during the late nesting period for mountain bluebirds. Together, these results indicate that the effects of conspecific and heterospecific neighbours on reproductive success are species-specific and vary depending on the phase of reproduction.

INTRODUCTION

Nest box programs have been instrumental to the recovery of secondary-cavity nesting species that have lost natural nesting habitat due to introduction of invasive species, centuries of deforestation, and land-use change (Hardin and Evans 1977; Munro and Rounds 1985). Despite the success of these programs, relatively little work has examined the behavioural and reproductive consequences of the density and distribution of nest boxes. These consequences could be significant, given that adding nest boxes to the landscape increases

species richness and nesting density (Twedt and Henne-Kerr 2001). The impact of neighbour distribution and density on reproductive success may vary by species and while conspecific neighbours may find themselves in direct competition for nesting sites, food, nesting material, and mates (both social and extra-pair), heterospecific neighbours may also experience competition for nest sites, nest material and/or food resources. Although the density and distribution of neighbours may have negative impacts on reproductive success, neighbours, whether heterospecific or conspecific, may also provide direct benefits in the form of defence from predators.

Competition from conspecific neighbours spans the entire breeding season and can directly impact reproduction (Jiang et al. 2022). The period of territory establishment often provides the first opportunity for conspecific neighbours to interact during the breeding season. In some species, conspecific neighbours engage in aggressive interactions such as posturing, increased singing, and physical contact (Hinde 1956; Tumulty et al. 2018). Aggressive behaviours between neighbours during the early parts of the nesting period can have negative consequences, particularly during egg laying and incubation. For example, Deeming et al. (2017) found that the clutch sizes of Eurasian blue tits (*Cyanistes caeruleus*) decreased as the distance to a conspecific's nest decreased. However, aggressive behaviours often become less frequent as familiarity with neighbours increases and as territorial boundaries become established (Temeles 1994; Tumulty et al. 2018). This tolerance of neighbours was described by Fisher (1954) as the "dear enemy hypothesis". Unfamiliar individuals that enter an established territory are typically met with aggression by the territory holder (Galeotti and Pavan 1993; Temeles 1994; Tumulty et al. 2018). Diminished aggression toward an established neighbour likely occurs because these behaviours are energetically costly (Ydenberg et al. 1988; Tumulty et al. 2018) and energy saved from reduced aggression toward a familiar neighbour can be redirected elsewhere.

Despite the potential energetic and reproductive costs, conspecific neighbours can also have positive impacts on survival and reproduction. Especially in colonial or semi-colonial nesting species, behaviours such as mobbing and reciprocal nest defence can benefit nesting pairs and neighbours alike (Ligon 1983; Krams et al. 2008; Russell and Wright 2009; Krama et al. 2012). In addition to nest defence, neighbours can enhance foraging efficiency

through information transfer—a pattern demonstrated in colonially nesting cliff swallows (*Hirundo pyrrhonota*) (Brown 1988) and European bee-eaters (*Merops apiaster*) (Campobello and Hare 2007). Another potential benefit to nesting in high densities could be increased breeding synchrony leading to predator swamping (e.g., Descampes 2019). Alternatively, nesting at high density with associated high reproductive success may simply be a by-product of individuals selecting the same high-quality resources (Danchin and Wagner 1997).

The effects of heterospecific neighbours on nesting birds is highly variable across species. In some cases, the presence of heterospecific neighbours may result in aggressive interference and competition for food or nest sites (Grether et al. 2017). However, aggressive interspecific interactions can also occur as a misdirection of aggression toward conspecifics, resulting in resource partitioning (Ley et al. 1997) and territory loss, both of which typically have a negative impact on the fitness of the individuals involved (Grether et al. 2017; but see Jiang et al. 2022). As a result of aggressive interactions, heterospecific neighbours can interfere with reproductive success, particularly during the territory establishment, mate acquisition, and incubation phases of the nesting period (Gröning and Hochkirch 2008; Campobello et al. 2015). However, the impacts of interference on reproductive success can be mitigated through increased neighbour distance, which would reduce the frequency of heterospecific interactions (Kuno 1992).

Though heterospecific neighbours can have detrimental effects, in some cases, individuals may actively seek out heterospecific neighbours when selecting a nest site (Quinn et al. 2003; Kivela et al. 2014). The presence of heterospecific individuals in an area may be used as an indicator of high-quality habitat, thus attracting other species to that location (Monkkonen and Forsman 2002). Some species can recognize the alarm calls of their heterospecific neighbours and may participate in calling even if they have not detected the threat themselves (Altmann 1956; Dutour et al. 2017). Nesting near species with more aggressive behavioural tendencies toward potential threats can result in improved reproductive success (Richardson and Bolen 1999; Quinn and Ueta 2008; Magrath et al. 2015). Indeed, Haff and Magrath (2013) reported that the response of white-browed scrubwren (*Sericornis frontalis*) fledglings as young as two weeks old to the alarm call of a

heterospecific neighbour was the same as that made to a conspecific alarm call. Thus, if individuals can recognize heterospecific alarm calls, the presence of heterospecific neighbours can provide protection from potential nest predators (Lawson et al. 2020). While often reported as either a cost or a benefit, the influence of heterospecific neighbours on reproductive success can change during the breeding season. Swift et al. (2018) observed improved hatching rate of Hudsonian godwit (*Limosa haemastica*) eggs through indirect nest defense when located near mew gull (*Larus canus*) colonies, but mew gulls later became predators, with a decrease in godwit chick survival at nests near mew gull colonies.

Nest box networks comprised of conspecific and heterospecific neighbours provide an ideal situation for monitoring the reproductive consequences of neighbour density and proximity. Mountain bluebirds (*Sialia currucoides*) and tree swallows (*Tachycineta bicolor*) are migratory songbirds that commonly breed in nest boxes in open grasslands with forest edges. Although tree swallows have a wider distribution across North America, both species occur together across much of the mountain bluebird's range. As secondary cavity nesters, both species compete directly for nest sites; however, they do not compete directly for food resources as mountain bluebirds are primarily ground foragers (Johnson and Dawson 2020) and tree swallows feed on flying insects (Winkler et al. 2020). Mountain bluebirds typically return to the breeding grounds approximately two weeks earlier than tree swallows, giving them a head start on establishing territories. Although tree swallows arrive later than mountain bluebirds, their aggressive and persistent harassment often results in successful acquisition of nest boxes from bluebirds that have begun nest construction (Meek et al. 1994; Wiebe 2016). Once nest box ownership by a bluebird is established and the first egg is laid, tree swallows rarely usurp the bluebird pair from their nest (S. Joly, personal observation). Both species will defend their nests from threats by diving, bill snapping and alarm calling; however, tree swallow alarm calls attract neighbouring tree swallows to join in mobbing of the perceived threat (Winkler et al. 2020), whereas those of bluebirds do not.

In this study, we investigated the effects of proximity and abundance of conspecific and heterospecific neighbours on the reproductive success of mountain bluebirds and tree swallows in nest boxes. If tree swallows and mountain bluebirds compete for nest sites, we predicted that during the early part of the nesting period, increased abundance of tree

swallow neighbours would reduce hatching rate in mountain bluebirds by disrupting incubation. However, as a result of earlier nest initiation by mountain bluebirds, we did not expect clutch size for either species to be affected by neighbours. Similarly, we did not expect bluebird neighbours to influence hatch rate at tree swallow nests as bluebird nests are already established when swallows begin nesting. Later in the nesting period, if both species benefit from mutual nest defense through alarm calling and/or mobbing of potential threats or if birds cluster in higher densities in higher quality habitat, we predicted fledging rate would be positively associated with the presence of both conspecific and heterospecific neighbours.

METHODS

Field Data Collection

To examine mountain bluebird and tree swallow activity at nest boxes, we used information gathered by members of the Kamloops Naturalist Club between 2012 and 2019 for 14 preexisting routes comprising a total of 294 nest boxes in the region surrounding Kamloops, British Columbia (50.6754° N, 120.3273° W). Routes were established in areas of grassland, forest edge, and agricultural activity and boxes were typically mounted to fence posts. When the nestbox routes were established, boxes were placed along fence lines where they could be accessed by volunteers with the permission of private landowners. Due to our reliance on volunteers and because nearly all boxes were located next to private land, we were not able to search for natural nest sites in this study; nonetheless, we expect these to be few given the loss of natural habitat throughout our study area. Although we did not specifically search for them, we have encountered only one natural nest site in over a decade of study.

Each breeding season (April to August), volunteers using a standardized data collection protocol checked the nest boxes on a weekly basis, recording the date of observation and activity at each nest box. Of the 14 routes, three routes were routinely checked at intervals greater than seven days and were not included in our study. Occupied nest boxes were checked more frequently (not more than five days between checks) once the first egg was laid. For occupied boxes, the species was recorded, along with the number of eggs, nestlings, and fledglings observed during each check. Fledging of nestlings was

determined based on evidence at the nest box, with the number of fledglings recorded based on the number of nestlings observed at the penultimate visit. Nestlings were determined to have fledged when the nest was noticeably flattened, the inside walls of the box were whitewashed with fecal material, and feather sheath flakes could be observed (Pearman 2005). We determined that nestlings did not fledge if these criteria were not met or if the nest box was empty but not enough time had passed after hatching for the nestlings to have reached fledging age. Unhatched eggs and dead nestlings remaining in the nest box post-fledging were also counted. Note that at our study site, adults do not remove these from the nest; however, eggshells could be removed from the nest without detection resulting in some error in estimates of hatching and fledging success.

In 2019, we recorded the GPS coordinates for all nest boxes on each of the 11 routes using a Garmin eTrex 10 handheld unit. If a nest box was moved between 2012 and 2019, we recorded the GPS coordinates for the previous location and the year the change was made. We created a distance matrix using R version v. 3.6.2 (R Core Team 2019) using the *geosphere* package (Karney 2013) to determine the straight-line distances among all 294 nest boxes in each year. We used the straight-line distances (m) to determine the distance to the nearest conspecific and heterospecific neighbour (Appendix Table B.1) and the number of conspecific and heterospecific neighbours within 250m and 500m (Appendix Table B.2) of each active mountain bluebird (n=469) and tree swallow (n=637) nest. We selected these distance intervals as songbirds will often travel more than 500m from their territory in search of extra-pair copulation (Dunn et al. 1994; Norris and Stutchbury 2001; Balenger et al. 2009), suggesting that they encounter at least conspecifics within this range. Similarly, GPS-tracked female tree swallows have been found to forage up to 2825m from the nest, with 90% of locations within 500m of the nest (Elgin et al. 2020). These findings are consistent with our own observations of banded individuals detected more than 3000m from their nest box (S. Joly, pers. obs.). To be considered a neighbour, a nest box must have been active and contained eggs or nestlings at the same time as the focal nest. We excluded nests with a first egg date more than 35 days after the penultimate egg of the focal nest was laid. This timespan allowed for a 14-day incubation period and 21-day nestling period for both mountain bluebirds (Johnson et al. 2013) and tree swallows (Austin and Low 1932). Although mountain bluebirds (Johnson and Dawson 2020) and tree swallows (Winkler et al.

2020) may renest or have a second nest in a single season, we did not include known second nests or renests in this study.

Statistical Analysis

To examine the influence of neighbours on mountain bluebird (hereinafter: bluebird) and tree swallow (swallow) reproductive success, we developed a series of generalized linear mixed models (GLMM) that related the number of conspecific and heterospecific nests within 250m and 500m, and distances to the nearest conspecific and heterospecific neighbours, to clutch size, hatching success, and fledging success. Year and box number were included as a random effect in each model. Because all nests had at least one egg, we used a quasi-Poisson GLMM to analyze the effect of neighbours on clutch size. We used GLMMs with a binomial error distribution (Brooks et al. 2017) to analyze the influence of neighbours on hatching and fledging success. We ranked each model using Akaike's information criterion (AICc). Models with a ΔAICc ≤2 were considered competitive. We considered variables to be important if model-averaged 95% confidence intervals in the top models did not overlap zero. Due to high levels of correlation (r = 0.7 - 0.9) between the number of nests at 250m and 500m within a species, we did not include multiple distances for the same species in any model. Thus, for a given reproductive variable and a given species, we ranked all subsets of models that contained the number of bluebird and tree swallow nests within either 250m or 500m; distance to nearest bluebird nest; and distance to nearest swallow nest. This resulted in a total of 28 models (including the null model). We did not detect any overdispersion in our models. All statistical analyses were performed in R (R Core Team 2019) using R studio (Rstudio 2020).

RESULTS

Early Nesting Period (Clutch Size and Hatching Success)

Bluebirds—Distance and proximity of neighbours had no effect on clutch size in bluebird nests (Table 2.1), with all model-averaged 95% confidence intervals in the top models overlapping zero. The top model explaining variation in hatching success included the number of swallow nests within 500m, and the distance to the nearest swallow neighbour (Table 2.1). The hatching rate in bluebird nests was lower when there were more swallow

nests within 500m (Table 2.2) but was higher when the nearest swallow nest was closer (Table 2.2). The model-averaged 95% confidence intervals for the number of tree swallow nests within 500m and the distance to the nearest swallow nest did not overlap zero (Table 2.2).

Table 2.1. Summary of the top ranked models explaining associations between tree swallow (TRES) and mountain bluebird (MOBL) neighbours and variability in reproductive success measures at mountain bluebird nests (≤2 ΔAICc). Total number of models tested was 28.

Model category Top models	AIC_c	ΔAIC_c	AIC_c weight
Clutch Size			
Null model	1704.51	0.00	*0.16*
Hatching Success			
TRES 500 + Nearest TRES	1381.29	0.00	*0.38*
MOBL 500 + TRES 500 + Nearest TRES	1381.74	0.45	*0.30*
MOBL 500 + TRES 500 + Nearest TRES + Nearest MOBL	1382.78	1.48	*0.18*
TRES 500 + Nearest TRES + Nearest MOBL	1383.28	1.99	*0.14*
Fledging Success			
MOBL 500 + TRES 500 + Nearest MOBL	1724.95	0.00	*0.54*
MOBL 500 + TRES 500 + Nearest TRES + Nearest MOBL	1725.35	0.39	*0.44*

Table 2.2. Model-averaged parameter estimates and 95% confidence intervals for neighbour variables included in models with a ΔAICc of ≤2 that explain variation in reproductive success of mountain bluebirds in nest boxes. Bolded values indicate confidence intervals that do not overlap 0.

	Clutch Size	Hatching Success	Fledging Success
TRES within 250m	0.002 (-0.026, 0.047)		
TRES within 500m	0.001 (-0.017, 0.026)	**-0.266 (-0.361, -0.171)**	**0.473 (0.301, 0.646)**
MOBL within 250m			
MOBL within 500m	-0.001 (-0.032, 0.022)	-0.044 (-0.22, 0.039)	**0.324 (0.127, 0.521)**
Nearest TRES nest		**-0.403 (-0.585, -0.221)**	0.081 (-0.085, 0.443)
Nearest MOBL nest	0.003 (-0.022, 0.056)	-0.044 (-0.259, 0.127)	**0.546 (0.308, 0.785)**

Tree Swallows—We found that neither proximity nor number of conspecific or heterospecific neighbours had an influence on clutch size; the 95% confidence intervals for all neighbour variables overlapped zero (Table 2.3, Table 2.4). The top model explaining variation in hatching success for swallows included the number of bluebird nests within 500m, and the distance to the nearest bluebird neighbour (Table 2.3). Hatching rate was higher when the nearest tree swallow nest was closer and as the number of bluebird neighbours within 500m increased (Table 2.3, Table 2.4). However, tree swallow hatching rate increased as the distance to the nearest bluebird neighbour increased (Table 2.5). The model-averaged 95% confidence interval for the number of bluebird nests within 500m, the distance to the nearest bluebird neighbour, and the distance to the nearest tree swallow neighbour did not overlap zero (Table 2.4).

Table 2.3. Summary of the top ranked models that explain the influence of tree swallow (TRES) and mountain bluebird (MOBL) neighbours on reproductive success at tree swallow nests (≤2 ΔAICc). Total number of models tested was 28.

Model category Top models	AIC_c	ΔAIC_c	AIC_c weight
Clutch Size			
Null Model	1704.51	0.00	*1.00*
Hatching Success			
MOBL 500 + Nearest MOBL	2422.42	0.00	*0.39*
MOBL 500 + Nearest TRES + Nearest MOBL	2424.34	1.92	*0.15*
Fledging Success			
MOBL 500 + Nearest MOBL	2025.61	0.00	*0.13*
Nearest MOBL	2025.95	0.33	*0.11*
Null Model	2026.57	0.95	*0.08*

Table 2.4. Model-averaged parameters estimates and 95% confidence intervals for neighbour variables included in models with a ΔAICc of ≤2 that explain variation in reproductive success of tree swallows in nest boxes. Bolded values indicate confidence intervals that do not overlap 0.

	Clutch Size	Hatching Success	Fledging Success
TRES within 250m			
TRES within 500m			**0.002 (0.069, 0.102)**
MOBL within 250m			0.007 (-0.142, 0.297)
MOBL within 500m		**0.156 (0.031, 0.28)**	0.066 (-0.042 0.267)
Nearest TRES nest		**-0.008 (-0.189, -0.132)**	0.004 (-0.155, 0.234)
Nearest MOBL nest		**0.333 (0.143, 0.523)**	0.159 (-0.01, 0.433)

Late Nesting Period (Fledging Rate)

Mountain Bluebirds—The top model explaining variation in the fledging rate for mountain bluebird nestlings included the number of bluebird nests within 500m, the number of swallow nests within 500m, and the distance to the nearest bluebird neighbour (Table 2.1). The fledging rate of mountain bluebird nestlings was higher when there were more bluebird nests within 500m (Table 2.2). However, bluebird fledging rate also increased as the distance to the nearest conspecific neighbour increased (Table 2.2). Mountain bluebird fledging rate was also positively associated with the number of swallow nests within 500m (Table 2.2). The model-averaged 95% confidence interval for the bluebird and swallow abundance variables and the distance to the nearest bluebird neighbour did not overlap zero (Table 2.2).

Tree Swallows—While the fledging rate of swallow nestlings was best explained by the number of bluebird nests within 500m and the distance to the nearest bluebird neighbour (Table 2.3), the model-averaged 95% confidence intervals for both neighbour abundance and distance overlapped zero (Table 2.4).

Table 2.5. Summary of the effects of neighbour abundance and proximity on the reproductive success of mountain bluebird (MOBL) and tree swallows (TRES). Positive (+) indicates a positive effect on reproduction, while negative (-) indicates a negative effect on reproduction. For distance, a positive (+) effect indicates that having neighbours in closer proximity (shorter nearest neighbour distance) is associated with higher reproductive success.

	Clutch Size		Hatching Success		Fledging Success	
	MOBL	**TRES**	**MOBL**	**TRES**	**MOBL**	**TRES**
TRES within 250m						
TRES within 500m			-		+	+
Distance to Nearest TRES			+	+		
MOBL within 250m						
MOBL within 500m				+	+	
Distance to Nearest MOBL				-	-	

DISCUSSION

Conspecific and heterospecific neighbours can have different effects on reproduction and these effects tend to manifest in a species-specific manner and may vary over the breeding period (Forsman et al. 2002; Krams et al 2008; Harris and Siefferman 2014). Here, we concurrently investigated how the proximity and abundance of conspecific and heterospecific neighbours were associated with reproductive metrics of both mountain bluebirds and tree swallows. Results were complex but generally aligned with our specific predictions; the abundance of heterospecific neighbours was negatively associated with reproductive metrics in mountain bluebirds but positively associated with reproductive success in tree swallows during the early nesting period (Table 2.5). However, while conspecific and heterospecific neighbour abundance was associated with higher reproductive success (i.e., fledging rate) during the later stages of the nesting period for bluebirds (Table 2.5), we found no effect of heterospecific neighbours on the fledging rate of tree swallows (Table 2.5). Surprisingly, we found contrasting effects of nearest neighbour distance and abundance—having a nearest neighbour in close proximity was positively associated with hatching success, but negatively associated with fledging success.

For mountain bluebirds, we observed a negative effect of heterospecific neighbour abundance during the early nesting period. These results are consistent with our predictions; the decrease in hatching rate of mountain bluebird eggs may reflect an increase in frequency

of defensive behaviours toward heterospecific neighbours. Because tree swallows begin nesting later in the spring than mountain bluebirds, tree swallows may find themselves in direct conflict with established bluebirds that are in nest building and/or egg-laying stages of the nesting cycle. Both male and female mountain bluebirds will vigorously defend their nest from tree swallows but only the female incubates the eggs (Johnson and Dawson 2020). As a result, reduced incubation time and increased exposure of the eggs during times when females are chasing away intruders can increase the risk of egg failure (Webb 1987). For example, Brazil-Boast (2011) observed that nest defensive interactions by Gouldian finches (*Erythrura gouldiae*) toward long-tailed finches (*Poephila acuticauda*) reduced Gouldian finch egg and nestling success as time and energy was diverted from parental care. Surprisingly, however, for bluebird hatching success, we found a positive effect of having tree swallow neighbours in close proximity. Though the mechanism remains unclear, one potential explanation is that a single neighbour in close proximity may result in relatively low conflict but have the benefit of increased nest defence through early detection of threats (Grabowska-Zhang et al. 2012). Indeed, Winkler (1994) found that most tree swallow neighbours that came to defend against a predator decoy at a neighbour's nest came from less than 75m away, and local density of tree swallow nests did not affect the numbers of defending neighbours recruited.

The hatch rate of tree swallow eggs was positively associated with the number of mountain bluebird neighbours. However, as the distance to the nearest bluebird neighbour increased, hatching success at tree swallow nests improved even further. These results indicate while tree swallows may benefit from having bluebird neighbours through improved threat detection, the benefit diminished if the neighbour was too close. As above, this apparent contradiction may indicate a benefit to having bluebirds as neighbours through predator defence behaviours. Conspecific neighbour abundance had no influence on hatching rate at tree swallow nests. Tree swallows will aggressively defend their nest site from conspecifics within a radius of 10 – 15m (Winkler et al. 2020). As we had only 22 of 637 tree swallow nests within 20m of a conspecific neighbour, most nests were likely too far away to have experienced reproductive interference at the densities observed at our study site. While conspecific neighbour abundance did not influence tree swallow hatch rate, we did observe an increase in hatching rate as the distance to the nearest conspecific neighbour decreased.

This improvement may be the result of threat detection by a nearby neighbour (Winkler 1994; Grabowska-Zhang et al. 2012).

Consistent with our predictions, we observed a positive relationship between neighbour abundance and reproductive success in mountain bluebirds during the late nesting period. Though this pattern could result from shared nest defence (Winkler 1994; Grabowska-Zhang et al. 2012), it could also arise as an effect of habitat quality and resource availability (Jones et al. 2014). Higher quality habitat which can support more nesting pairs than lower quality habitat (Probst and Hayes 1987), may improve nest success (Vickery et al. 1992; Weinberg and Roth 1998), and may reduce foraging time, leading to increased provisioning rates by parents (Brawn 1991). Thus, the relationship between abundance of conspecific neighbours and reproductive success may reflect individuals nesting at higher densities in higher quality habitat. We did, however, find that having a conspecific neighbour in close proximity appeared to have a negative effect on the fledging rate of mountain bluebirds (Table 5). Although higher quality habitat can support a higher density of breeding pairs, the likelihood of reproductive interference by conspecific neighbours increases as the distance between neighbours decreases (Hinde 1956). The negative association of reproductive success and distance to the nearest conspecific neighbour may thus be the result of direct competition and reproductive interference. However, mountain bluebird breeding territory size is unknown (Johnson and Dawson 2020), making it difficult to infer the minimum distance at which reproductive interference may occur.

Not surprisingly, mountain bluebird neighbour abundance had no influence on tree swallow fledging rate. With an average of 14 days head start on their tree swallow neighbours, many bluebird nestlings have fledged, and adults are no longer defending nests by the time trees swallows are provisioning nestlings. Fledging success of tree swallows was positively influenced by conspecific neighbour abundance. Tree swallow nesting density depends greatly on nest site availability, and while tree swallows have been observed nesting in closer proximity (Hussell 2012) than we have in our study site, high quality habitat with high insect abundance may explain the increase in fledging success as conspecific neighbour abundance increases. Also, familiarity with conspecific neighbours can reduce aggressive interactions between neighbours (Fisher 1954), allowing more time for nestling provisioning.

Although the abundance of tree swallows appeared to have a negative effect on mountain bluebird reproduction during the early nesting period, abundance of tree swallows was positively associated with fledging rate. Mountain bluebirds and tree swallows employ different foraging techniques (Johnson and Dawson 2020; Winkler et al. 2020) and therefore are not in direct competition for food resources while provisioning their nestlings. An increase in fledging rate of mountain bluebird nestlings may result from the indirect nest defence provided by the aggressive mobbing behaviours exhibited by tree swallows (Winkler 1994; Russell and Wright 2009). Alternatively, higher fledging rate may simply be a by-product of both species selecting high-quality habitat with abundant resources for both species.

If reproductive interference is occurring through density-dependent competition, leading to reduced reproductive success of close neighbours, this could explain the spatial distribution of pairs across suitable habitat. Once territories are established, however, this spatial distribution across the landscape could reduce time spent engaging in aggressive interactions and thus increase the time parents can spend provisioning nestlings (Beletsky and Orians 1989; Jones et al. 2014). Detailed observations of tree swallow and mountain bluebird responses to conspecific and heterospecific nest defence behaviour would further our understanding of the impacts these behaviours have on the reproductive success of neighbours. Additional information on territory sizes and levels of nest site fidelity in these species, as well as assessment of the quality of the habitat in this study area would improve our understanding of neighbour interaction and distribution. Our results may have implications for researchers and naturalist groups establishing nest box programs. For instance, in areas of high mountain bluebird density and low tree swallow density, close spacing of nest boxes may be advantageous. Alternatively, in areas with higher tree swallow density, spacing of boxes at greater distances may reduce negative conspecific and heterospecific interactions.

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CHAPTER 3: CLOSE, BUT NOT TOO CLOSE: CONTRASTING EFFECTS OF NEIGHBOUR PROXIMITY AND ABUNDANCE ON EXTRA-PAIR PATERNITY IN MOUNTAIN BLUEBIRDS (*SIALIA CURRUCOIDES*)

ABSTRACT

For socially monogamous songbirds, the frequency of extra-pair paternity is often linked to the density and proximity of conspecific neighbours. Opportunities for extra-pair copulations increase as neighbour abundance increases, yet for males, increased neighbour abundance can also require increased mate-guarding to safeguard their own paternity. The mountain bluebird (*Sialia currucoides*) is a socially monogamous songbird that commonly breeds in open woodlands and grasslands across western North America and has relatively high rates of extra-pair paternity. In this study, we examine the influence of neighbour abundance and proximity on the occurrence and proportion of extra-pair offspring in mountain bluebird nests. We found that 54% of mountain bluebird nests contained extra-pair offspring. Conspecific neighbour abundance at distances of 500m and 1000m was positively associated with the occurrence and proportion of extra-pair offspring at focal nests. However, the likelihood of extra-pair offspring was negatively associated with neighbour abundance within 250m. These findings are consistent with other studies in which rates of extra-pair paternity increase with population density and opportunities for multiple mating; however, our results also suggest that when birds nest in close proximity, males may increase their mate-guarding efforts to secure paternity at their own nest.

INTRODUCTION

Social monogamy is a common reproductive strategy employed by songbirds, in which both the male and the female cooperate in the rearing of offspring. The adjective "social" is added because genetic analysis has revealed that socially monogamous songbirds frequently engage in extra-pair copulation and the putative male is often not the sire of all offspring in his nest (Griffith et al. 2002; Brouwer and Griffith 2019). This mixed mating strategy is extremely common with more than 80% of songbird species studied exhibiting some level of extra-pair paternity (Brouwer and Griffith 2019). The rate of extra-pair paternity varies greatly, with some species engaging in little to no extra-pair copulations (Petrie and Kempenaers 1998) and others

with greater than 70% of broods containing extra-pair nestlings (Dixon et al. 1994; Mulder et al. 1994; Balenger et al. 2009b) and over 80% of nestlings resulting from extra-pair paternity (Hughs et al. 2003; Wang et al. 2021; Dunning et al. 2023). This remarkable variation in extra-pair paternity among socially monogamous birds has led to an explosion in studies examining both the causes and consequences of extra-pair paternity (Brouwer and Griffith 2019).

While many studies examine extra-pair paternity in relation to song (Hasselquist et al. 1996; Forstmeier et al. 2002; Benitez Saldivar et al. 2022), colouration (Eikenaar et al. 2011; Whittingham and Dunn 2016; Thibault et al. 2022), and other sexually selected traits (Lehtonen et al. 2009; Valcu et al. 2023), variation in extra-pair paternity may also be explained by the density and proximity of potential mates (Charmantier and Perret 2003; Stewart et al 2010; Mayer and Pasinelli 2013). For example, the rate of extra-pair paternity can depend greatly on the frequency and opportunity of encounters between females and extra-pair males. Not surprisingly, within colonial songbirds, increased density and proximity of potential nearby extra-pair partners is associated with higher frequency of extra-pair paternity (Birkhead et al. 1992; Brown and Brown 1996). Likewise, density can also positively influence the rate of extra-pair paternity in non-colonial songbirds (Krokene and Lifield 2000; Rowe and Weatherhead 2007; Mayer and Pasinelli 2013). However, these patterns can be complex, depending on the species under study. For example, in Mayer and Pasinelli's (2013) investigation of extra-pair paternity in reed buntings (*Emberiza schoeniclus*) in Switzerland, the authors found that the rate of extra-pair paternity increased with the abundance of conspecific neighbours and declined as the distance to the nearest neighbour increased (Mayer and Pasinelli 2013). In contrast, Schlicht et al. (2014) showed that in Eurasian blue tits (*Cyanistes caeruleus*), an increase in neighbour abundance reduced the likelihood of a male siring extra-pair offspring due to mate guarding and female-female aggression. As such, both the density of neighbours and the distance that females must travel to pursue extra-pair copulations likely interact to play an important role in the frequency of extra-pair paternity (Stewart et al. 2010; Schlicht et al. 2014).

Though the density and abundance of neighbours is often positively associated with extra-pair paternity (Birkhead et al. 1992; Brown and Brown 1996; Di Lecce et al. 2023), it is not always the nearest neighbour that is the sire of extra-pair offspring. Both males and females may travel considerable distances to seek out extra-pair copulations (Smith et al. 2020; Santema and

Kempenaers 2023), though the absolute distance traveled varies across species. In American robins (*Turdus migratorius*), extra-pair males sired offspring in nests an average of 74m from their own nest (Rowe and Weatherhead 2007), while some warblers and bluebirds have been observed travelling more than 2000m from their territory, likely in pursuit of extra-pair copulations (Norris and Stutchbury 2001; Balenger et al. 2009b; Kowalski 2024).

At the start of the breeding season, conspecific neighbours often engage in aggressive interactions as they secure resources such as food, nest sites and mates. These interactions vary from simple posturing to physical contact (Akcay et al. 2009; Tumulty et al. 2018). While many of these interactions occur as part of the establishment of territories (Temeles 1994; Gutiérrez-Carrillo et al. 2023), others are the result of individuals mate-guarding against intruders searching for extra-pair copulations (Akcay et al. 2009). Mate guarding males closely accompany their female, particularly during the period leading up to incubation (Norris and Stutchbury 2001) to intercept potential extra-pair males and to prevent females from engaging in extra-pair copulations (Kokko and Morrell 2005). While mate guarding may reduce the risk of lost paternity at the male's nest, it also reduces the potential for the male to engage in extra-pair copulations (Hasselquist and Bensch 1991). As the abundance of neighbours increases, the likelihood of interactions with neighbours also increases and territorial defense by males is heightened (Barrero et al. 2023).

Heterospecific neighbours can also cause reproductive interference, often as a result of aggressive interactions for resources (Botero-Delgadillo et al. 2015; Grether et al. 2017), which can have a negative impact on reproductive success as individuals compete for food and nest sites (Grether et al. 2017). Secondary cavity nesting birds often engage in aggressive interactions to acquire and defend nest sites (Slagsvold and Wiebe 2021). The partitioning of resources through aggressive interactions with heterospecific neighbours can be particularly impactful during the early breeding season when birds are establishing territories and finding mates (Groning and Hochkirch 2008; Joly et al. 2024). However, despite this potential for heterospecific neighbours to interfere with reproduction (e.g., through disrupting mate-guarding or reducing opportunities for extra-pair forays), little work has examined the influence of such neighbours on patterns of extra-pair paternity (Baldassarre et al. 2019).

In interior British Columbia, mountain bluebirds (*Sialia currucoides*) and tree swallows (*Tachycineta bicolor*) occupy nest boxes that are often in close proximity to each other. Previous work (Ch 2) demonstrated that the proximity and abundance of both conspecific and heterospecific neighbours is associated with reproductive success in both species. Tree swallow neighbours negatively influenced bluebird hatching rate but had a positive influence on fledging rate. However, whether neighbour proximity and abundance influences patterns of extra-pair paternity in mountain bluebirds remained unknown. Like all North American bluebirds, mountain bluebirds are socially monogamous and frequently engage in extra-pair copulation (Meek et al. 1994; Balenger et al. 2009b; Stewart et al. 2010; Smith et al. 2020). In fact, of the three *Sialia* species in North America, mountain bluebirds have the highest reported rate of extra-pair paternity, with more than 70% of nests in some studies containing at least one extra-pair offspring (Balenger et al 2009b).

In this study, we examine the influence of neighbour abundance and nearest neighbour proximity on the occurrence and proportion of extra-pair offspring at mountain bluebird nests. We hypothesize that an increase in conspecific neighbour abundance may lead to an increased opportunity for extra-pair copulations, resulting in a higher likelihood of extra-pair offspring at the nest and a greater proportion of extra-pair offspring in the nest. We also expect that as the distance to the nearest conspecific neighbour decreases, the opportunity for extra-pair copulations increases resulting in increased extra-pair paternity. While tree swallows and bluebirds compete for nest sites, an earlier start to the breeding season by bluebirds means we do not expect tree swallow neighbour abundance or proximity to affect extra-pair paternity in bluebirds.

METHODS

Field Methods

To examine breeding activity of mountain bluebirds and tree swallows, we monitored 122 nest boxes along four pre-existing routes that are part of the larger "Bluebird Trails" program run by a local naturalist club (Kamloops Naturalists Club) in Kamloops, British Columbia (50.6754° N, 120.3273° W) between 2012 and 2019 (Table 3.1). Routes were established in areas of grassland, forest edge, and agricultural land; boxes were typically mounted to fence posts adjacent to private land.

Table 3.1. Number of nest boxes for each route.

Route Name	Number of Nest Boxes
Dew Drop	43
Edith Lake Rd.	29
Jackson Rd.	20
Long Lake Rd.	30
Total	**122**

Each breeding season (April to August), we conducted nest checks at intervals of five days at maximum. During each check, we recorded the date of observation, the species present and the breeding activity at each nest box. For each active mountain bluebird (hereinafter: bluebird) and tree swallow nest we recorded the start date of nest construction, first egg date, clutch size, the number of nestlings, and the number of fledglings observed during each check. We also recorded the number of eggs that failed to hatch and nestlings that failed to fledge. Nest check intervals were reduced to not more than three days as hatching and fledging events approached.

Between 2012 and 2019 we acquired feather or blood samples from mountain bluebird adults and nestlings at 61 nests in 41 different boxes. We caught adult bluebirds at the nest box as they were feeding three-to-five-day old nestlings using a trap door mounted to the inside of the box entrance. We used this nestling age range as at this point the nestlings were no longer being brooded by the female yet were not mobile enough to meet the parents at the entrance to receive food; this meant they required the adults to fully enter the box to feed the nestlings. We banded each adult with a United States Geological Survey (USGS) numbered aluminum 1B or 1A band (Pyle 1997) and a unique combination of colour bands for field identification. We determined the age of all adults as either second year (SY) or after second year (ASY) based on the presence/absence of a moult limit within the greater primary coverts (Pyle 1997) and collected one tail feather (R3) for genetic analysis. We measured wing length (mm), tail length (mm) and tarsus length (mm) for all adults.

We applied a 1B or 1A (Pyle 1997) USGS numbered aluminum band to all live nestlings at 10-11 days of age and collected approximately 10 µl of blood from the ulnar vein. We used

hematocrit tubes to transfer each nestling's blood sample to a dry filter paper labelled with the nestling's band number, nest box number, and collection date. For all dead nestlings we collected a pin feather to be used for analysis.

We recorded the GPS coordinates for all nest boxes on each route using a Garmin eTrex 10 handheld unit. With these coordinates we created a distance matrix in R version v. 3.6.2 (R Core Team 2019) using the *geosphere* package (Karney 2013) to determine the straight-line distances among all 122 nest boxes. We used the straight-line distances (m) to determine the distance to the nearest conspecific and heterospecific neighbour and the number of conspecific and heterospecific neighbours within 250m, 500m, and 1000m of each active mountain bluebird nest. We selected these distance intervals as songbirds, including bluebirds, often travel 1000m or more from their territory in search of extra-pair copulation (Dunn et al. 1994; Norris and Stutchbury 2001; Balenger et al. 2009b). To be considered a neighbour, a nest box must have been active and contained eggs or nestlings at the same time as the focal nest. We excluded nests with a first egg date more than 35 days after the penultimate egg of the focal nest was laid. This timespan allowed for a 14-day incubation period and 21 day nestling period for both mountain bluebirds (Johnson et al. 2013) and tree swallows (Austin and Low 1932). Although mountain bluebirds (Johnson and Dawson 2020) may renest or have a second nest in a single season, we did not include second nests or renests in this study.

Laboratory Methods

We extracted genomic DNA from blood stored on filter paper or feather samples (basal portion of feather shaft) using a modified Chelex procedure (Burg and Croxall 2001; Walsh et al. 1991). To determine paternity, we used nine microsatellite loci (Table 2.1) isolated for mountain bluebird and other passerine species: *Cuu 2*, *Cuu 4*, *EABL 129*, *MOBL 87*, *Siala 37*, *SMex 6*, *SMex 8*, *SMex 10* and *SMex 13* (Boutin-Ganache et al. 2001; Ferree et al. 2008; Duckworth and Kruuk 2009). Genomic DNA was amplified in 10 µL reaction volumes containing colourless GoTaq® Flexi buffer (Promega), 0.2 mM dNTP, and 0.8 mM or 1 mM $MgCl_2$, 0.5 µM forward and reverse primer, 0.05 µM fluorescent M13 tag, 0.5 U GoTaq® Flexi DNA polymerase (Promega). The amplification profile consisted of a 2-minute denaturation at 94°C, 45 seconds (s) at 50°C and 1 minute at 72°C; followed by seven cycles of 1 minute at 94°C, 30 s at T_{m1} and 45 s at 72°C; before 28 cycles of 30 seconds at 94°C, 30 s at T_{m2} and 45 s at 72°C, and a final

five-minute elongation at 72°C. Annealing temperatures (T_{m1}/T_{m2}) differed for each primer set; we used a T_{A1} of 50°C and a T_{A2} of 52°C for the two-step annealing process for SMex 10 and Siala 37, while the remaining seven loci used a TA_1 of 55°C and a T_{A2} of 57°C for the two-step annealing process. PCR products were separated on 6% acrylamide gels on a LICOR 4300 DNA Analyzer (Licor Inc., Lincoln, NE). Alleles were scored by visual inspection and each run contained three known positive controls to ensure consistent scoring and amplification across gels. Allele frequencies were determined using the CERVUS 3.0.7 software package (Kalinowski et al. 2010). We determined a nestling to be extra-pair if we had a minimum of four microsatellite loci identified for that individual and if three or more loci did not match those of the within-pair male by two or more base pairs, depending on which loci was mismatched.

Table 3.2. Allelic variation for nine microsatellite loci used to assess extra-pair paternity of mountain bluebirds. The number of alleles in our population for each locus is given along with the observed (H_o) and expected (H_e) heterozygosities.

Locus	Size (bp)	Repeat length (bp)	Number of Alleles	H_o	H_e
Cuu2	130-155	2	15	0.868	0.893
Cuu4	100-140	2	21	0.854	0.923
EABL 129	180-228	2	20	0.831	0.879
MOBL 87	160-180	2	14	0.801	0.850
Sialia 37	280-320	4	12	0.706	0.706
SMex 6	155-175	4	17	0.881	0.922
SMex 8	240-290	4	7	0.739	0.761
SMex 10	222-262	4	11	0.773	0.808
SMex 13	151-187	4	13	0.721	0.876

Paternity assignment

We conducted paternity assignment using CERVUS 3.0.7 software (Kalinowski et al. 2010) with a strict confidence limit of 99%, a relaxed limit of 95%, and a 1% assignment error due to incomplete sampling of male genotypes. We estimated that we genotyped 50% of the male population based on our field observations of banded and unbanded individuals. For assignment, we included genotypes of 50 adult females, 45 adult males and 78 nestlings identified as extra-pair offspring. We removed from analysis ten individuals (two males, two females, and 6 nestlings) for which fewer than three loci were sampled.

Statistical analysis

To examine the influence of neighbours on extra-pair paternity of bluebird nestlings, we constructed a series of linear mixed models with binomial error distributions using the lme4 function (Bates et al. 2015) in R (R Core Team 2019). We used the proportion of extra-pair offspring and the presence of extra-pair offspring at the nest (yes/no) as our response variables and included fixed effects of number of conspecific and heterospecific neighbours within 250m, 500m, and 1000m, and distances to the nearest conspecific and heterospecific neighbours. In addition to neighbour abundance and proximity, we also included the age, wing length, tail length, and tarsus length of adults. Year and box number were included as random effects.

Because we were interested in the variable or combination of variables that best explained the presence and proportion of extra-pair young, we employed model selection using the dredge function within the multi-model inference (MuMln) package (Burnham and Anderson 2002) to create all possible combinations of fixed effects and we subsequently ranked all models using Akaike's information criterion (AICc). The top five models were considered competitive. We then used model averaging for factors identified in competitive models to examine the 95% confidence intervals of the parameter estimates. To compare body size metrics of the putative male to the extra-pair male, we conducted t-tests and paired t-tests. We did not detect high levels of correlation between variables (i.e., $r \leq 0.6$ in all cases) nor overdispersion in any of our models. All statistical analyses were performed in R (R Core Team 2019) using R studio (Rstudio 2020).

RESULTS

The average distance to the nearest conspecific neighbour was 813 ± 87.6m SD. Each year (2012 – 2019) of our study included at least one bluebird nest with extra-pair nestling(s) (Table 3.3). Of the 61 mountain bluebird nests, 54% (33 of 61) contained at least one extra-pair offspring and 44% (79 of 102) of nestlings were sired by extra-pair males. The average percentage of extra-pair nestlings per nest ranged from 10 – 60 percent across years (Table 3.4). Of the 33 nests with extra-pair offspring, only two nests (6%) contained extra-pair nestlings sired by the nearest neighbour (40.2m away) and each nest had extra-pair nestlings sired by the other's nearest neighbour. The average distance between the focal box and the extra-pair male's nest box was

2199 ± 1357.4m SD. Of the 33 bluebird nests with extra-pair nestlings assigned to a male, 69.7% (23/33) contained more than one extra-pair nestling with 65.2% (15/23) of those with nestlings sired by more than one extra-pair male (Table 3.5)

Table 3.3. Annual variation in the number of mountain bluebird nests with at least one extra-pair offspring over eight consecutive years (2012 – 2019).

	2012	2013	2014	2015	2016	2017	2018	2019
Nests with EPO	3	2	4	6	1	4	1	7
Total Nests	5	6	6	17	1	6	2	18

Table 3.4. Variation in the proportion of extra-pair offspring in mountain bluebird nests over eight consecutive years (2012—2019).

	2012	2013	2014	2015	2016	2017	2018	2019
Total Nests	5	6	6	17	1	6	2	18
Mean per nest	0.253	0.150	0.175	0.151	0.600	0.344	0.100	0.113
Std. Deviation	0.281	0.235	0.154	0.226		0.280	0.141	0.155
Minimum	0.000	0.000	0.000	0.000	0.600	0.000	0.000	0.000
Maximum	0.600	0.500	0.400	0.600	0.600	0.667	0.200	0.400

Table 3.5. The number of extra-pair male (EPM) sires of nestlings at nests containing more than one extra-pair nestling (n=23).

	1 EPM	2 EPMs	3 EPMs	4 EPMs
Nests with more than one EPO	8	10	4	1

Occurrence of extra-pair offspring

The abundance of conspecific neighbours within 250m was negatively associated with the occurrence of extra-pair offspring at bluebird nests (Figure 3.1). However, the likelihood of a bluebird nest having at least one extra-pair nestling increased as the number of conspecific nests within 500m and 1000m increased (Figure 3.1). The top model explaining variation in the occurrence of extra-pair offspring included the number of bluebird nests within 250m and 1000m (Table 3.6). The model-averaged 95% confidence intervals for the abundance of bluebird neighbours within 250m, 500m and 1000m did not overlap zero (Table 3.8). The abundance and proximity of tree swallow neighbours was not present in any top model.

Table 3.6. Summary of the top five models explaining associations between mountain bluebird (MOBL) neighbours and variability in the occurrence of extra-pair offspring at mountain bluebird nests.

Top models	AIC$_c$	ΔAIC$_c$	AIC$_c$ weight
MOBL 1000 + MOBL 250	77.0	0.00	*0.37*
MOBL 2500 + MOBL 500	78.5	1.57	*0.17*
MOBL 1000 + MOBL 250 + Nearest MOBL	78.6	1.66	*0.16*
MOBL 1000 + MOBL 250 + Female Wing	78.7	1.75	*0.16*
MOBL 1000 + MOBL 250 + Male Tail	79.0	2.00	*0.14*
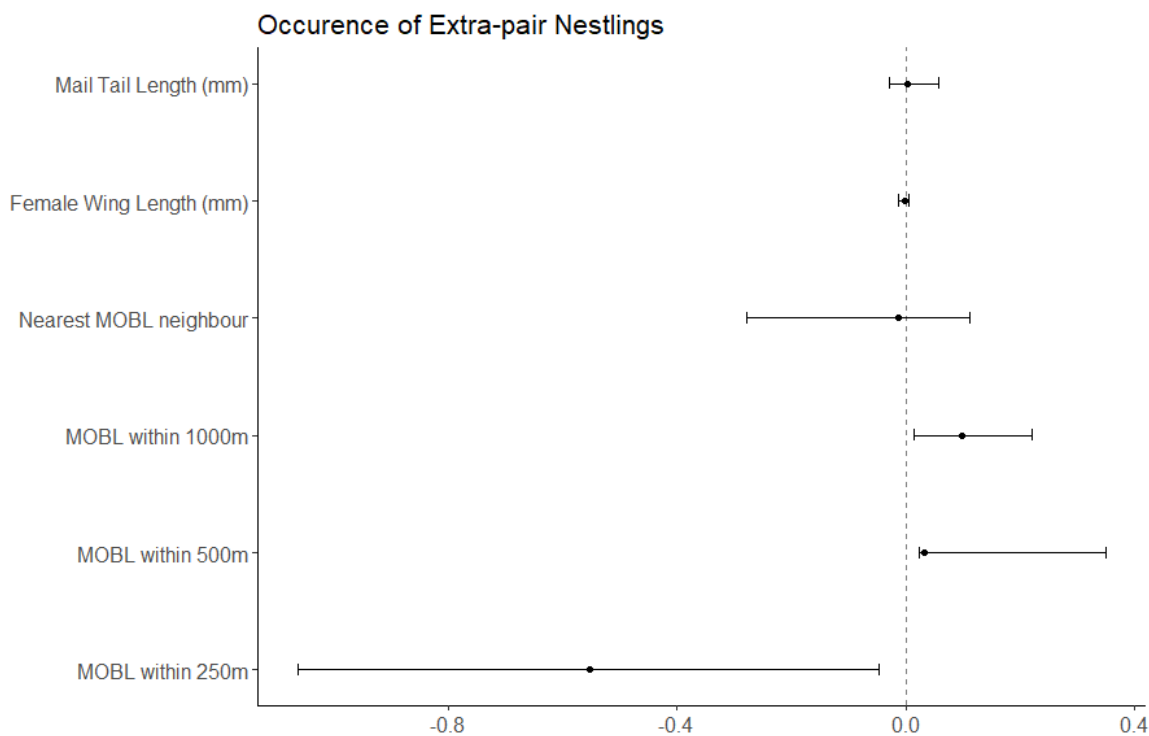
Figure 3.1. The model-averaged 95% confidence intervals of parameter estimates for conspecific neighbour abundance within 250m, 500m, and 1000m of the focal nest did not overlap zero for the occurrence of extra-pair nestlings: the data show that; nests with increased conspecific neighbour abundance within 250m were less likely to have extra-pair offspring while increased neighbour abundance within 500m and 1000m had higher probability of extra-pair nestlings.

Proportion of extra-pair offspring

The proportion of extra-pair offspring increased as the number of conspecific neighbours within 500m increased (Figure 3.2). We also observed that as the distance to the nearest conspecific neighbour increased, the proportion of extra-pair nestling within the brood decreased (Figure 3.2). The model-averaged 95% confidence intervals of the parameter estimates for neighbour abundance within 500m and the distance to the nearest neighbour did not overlap zero (Table 3.8). There was a marginal negative association between the proportion of extra-pair nestlings in bluebird nests and the number of conspecific nests with 250m and a positive association with the number of neighbours within 1000m (Figure 3.2). Neither the presence nor abundance of heterospecific neighbours were present in any top models.

Table 3.7. Summary of the top five models explaining associations between mountain bluebird (MOBL) neighbours and variability in the occurrence of extra-pair offspring at mountain bluebird nests.

Top models	AIC_c	ΔAIC_c	AIC_c weight
MOBL 1000 + MOBL 250	-7.0	0.00	*0.11*
MOBL 250 + MOBL 500	-6.7	0.35	*0.09*
MOBL 250 + Nearest MOBL	-6.0	1.04	*0.07*
MOBL 1000	-5.7	1.31	*0.06*
MOBL 250 + MOBL 500 + Male Tail	-5.7	1.34	*0.06*

Table 3.8. Model-averaged parameters estimates and 95% confidence intervals for neighbour variables included in the top five models with that explain variation in occurrence (Y/N) and proportion of extra-pair offspring (EPO) in mountain bluebird nest boxes. Bolded values indicate confidence intervals that do not overlap 0.

|	Occurrence of EPO (Y/N)	Proportion of EPO
MOBL within 250m	**-0.554 (-1.063, -0.046)**	-0.120 (-0.476, 0.012)
MOBL within 500m	**0.032 (0.023, 0.350)**	**0.030 (0.005, 0.152)**
MOBL within 1000m	**0.097 (0.014, 0.220)**	0.019 (-0.001, 0.089)
Nearest MOBL nest	-0.014 (-0.278, 0.112)	**-0.013 (-0.146, -0.001)**
Female Wing Length (mm)	-0.001 (-0.013, 0.006)	
Male Tail Length (mm)	0.002 (-0.029, 0.057)	0.002 (-0.008, 0.030)
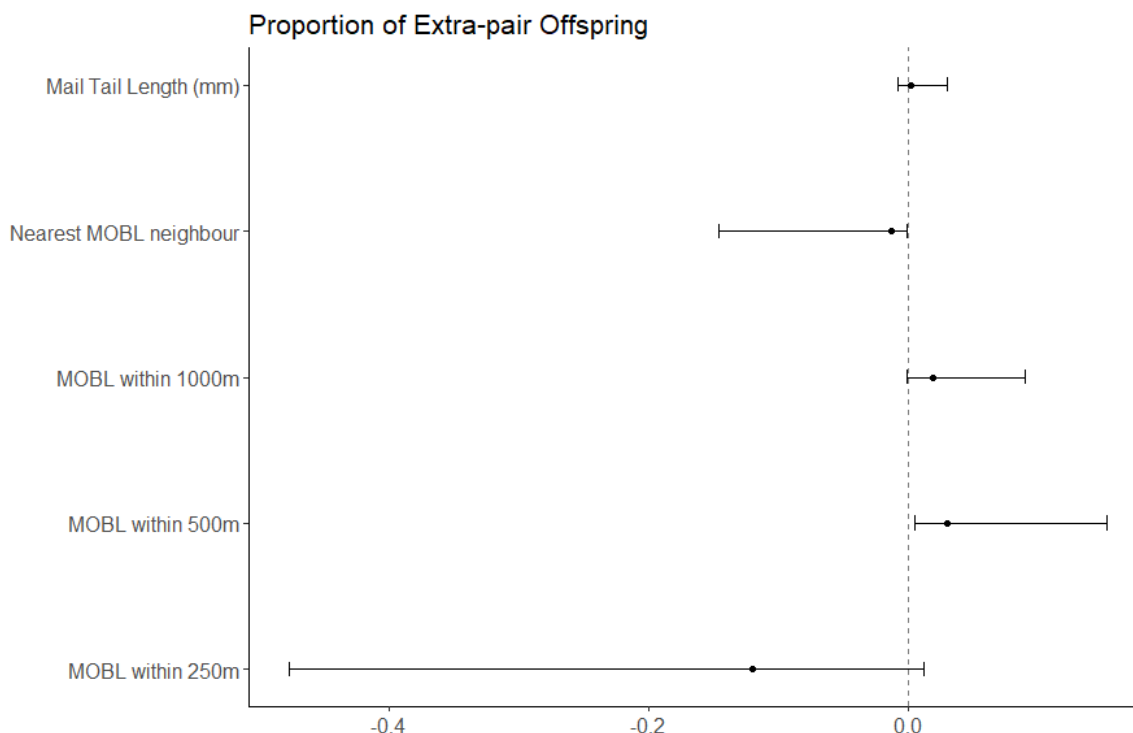
Figure 3.2. The model-averaged 95% confidence interval of parameter estimates for conspecific neighbour abundance within 500m and the distance to the nearest bluebird neighbour did not overlap zero. The proportion of extra-pair nestlings in mountain bluebird nests increased as number of conspecific nests within 500m increased and decreased as the distance to the nearest neighbour increased.

Although male tail length and female wing length appeared in our top five models, parameter estimates for adult bluebird size and age both overlapped zero (Tables 3.6 and 3.7). We conducted a series of t-tests to compare the weight, wing length, tail length, and tarsus length of males with extra-pair nestlings in their nests to males without extra-pair nestlings. We found no difference between the size of males with and without extra-pair nestlings in their nest (Table 3.9). When we compared the within-pair male to the sire of each extra-pair offspring in his nest using paired t-test, we found no significant difference in body size metrics (Table 3.10, Appendix Figure C.1). We also found that neither male or female age influenced the occurrence or proportion of extra-pair nestlings. In our study, 30% (3/10) of second year (SY) female's nests contained extra-pair nestlings while 49% (24/49) of after second year (ASY) females had extra-

pair offspring in their nests. For males, 48% (10/21) of younger (SY) male's nests contained extra-pair offspring and 43% (16/37) of older (ASY) males had extra-pair offspring in their nest. After second year males were more likely to sire extra-pair offspring than younger second year males (χ^2=4.24, p=0.04). Neither tree swallow neighbour abundance nor distance to the nearest tree swallow neighbour influenced the likelihood of extra-pair offspring or proportion of extra-pair nestlings at bluebird nests.

Table 3.9. Male mountain bluebirds with extra-pair nestlings (n=31) showed no difference in body metrics when compared to males without extra-pair nestlings (n=26) in their nests.

	Males with EPO Average (SD)	Males without EPO Average (SD)	t-value	df	p-value
Weight (gm)	28.95 (1.51)	29.16 (1.51)	-0.253	25	0.802
Wing length (mm)	114.8 (2.75)	115.1 (3.21)	-1.188	25	0.246
Tail Length (mm)	69.46 (3.67)	68.8 (2.83)	0.081	25	0.936
Tarsus Length (mm)	22.49 (1.11)	22.34 (0.85)	0.878	25	0.388

Table 3.10. Comparison of body size metrics of within-pair male (WM) to the sires (EM) of extra-pair offspring in their nest (n=43).

Measure 1		Measure 2	t-value	df	p-value
WM Weight	-	EM Weight	0.538	42	0.593
WM Wing	-	EM Wing	-0.793	42	0.432
WM Tail	-	EM Tail	0.220	42	0.827
WM Tarsus	-	EM Tarsus	0.760	45	0.451

DISCUSSION

Like other populations of mountain bluebirds (e.g., Balenger et al. 2009b), rates of extra-pair paternity in our study population were high, with 54% of nests containing extra-pair offspring and 44% of all nestlings sired by extra-pair males. Because conspecific neighbour abundance and proximity can influence the occurrence and proportion of extra-pair nestlings (Westneat and Sherman 1997; Stewart et al. 2010), we investigated the influence of neighbour abundance and the distance to the nearest neighbour on the occurrence and proportion of extra-pair nestlings. As predicted, the occurrence of extra-pair offspring in mountain bluebird nests was positively associated with the abundance of conspecific neighbours within 500m and 1000m. In addition,

the proportion of nestlings sired by extra-pair males increased as the abundance of conspecific neighbours within 500m increased. In contrast, however, the likelihood of extra-pair paternity decreased when a conspecific nest was in closer proximity.

Though most theoretical and empirical evidence (Stewart et al. 2010; Arrieta et al 2022; Di Lecce et al. 2023) suggests that an increase in neighbour density should result in higher rates of extra-pair paternity, high local densities may reduce the likelihood of extra-pair offspring in species that actively engage in mate guarding (Thusius et al. 2001; Schlicht et al. 2015) and territorial defense (Currie et al. 1998; Barrero et al. 2023; Beccardi at al. 2023). Although extra-pair paternity increased as neighbour abundance increased at distances of 500m and 1000m, we observed a decline in the occurrence of extra-pair offspring as neighbour abundance increased within 250m of the focal nest. Since they are secondary cavity-nesters, mountain bluebird territory size varies with the availability of suitable nest sites (Power 1966). Bluebirds will vigorously defend their nest and mate from conspecific intruders (Johnson and Dawson 2020). To reduce the likelihood of extra-pair copulations, males will often follow the females closely and mate guard, particularly during periods when the female is most receptive (Dickinson and Leonard 1996; Kokko and Morrell 2005; Valera et al. 2003). Male western bluebirds (*Sialia mexicana*) stayed closer to their mates in the period leading up to incubation and in areas with higher densities of males (Dickinson and Leonard 1996). As such, one possibility is that the reduction in extra-pair paternity as nearby neighbour abundance increased may stem from an increase in behaviours such as mate guarding and territory defense that both reduce extra-pair paternity at the focal nest and restrict time available for males to pursue extra-pair copulations.

While neighbour abundance is often associated with increased rates of extra-pair paternity (Mayer and Pasinelli 2013; Di Lecce et al. 2023), extra-pair sires are not necessarily the closest neighbour (Charmantier and Perret 2003; Balenger et al. 2009b). In a study on mountain bluebirds in Wyoming, USA, Balenger et al (2009b) found just 15% of extra-pair males sired offspring in the nearest nest to their own and the distance to the extra-pair males nest ranged from 99 – 3624m with an average distance of 812m. The average distance to the nearest bluebird nest in our study was 813 ± 87.6m SD. However, we found that only 6% of the nests had offspring sired by their nearest neighbour and the average distance to the extra-pair male's nest was 2199m ± 1357.4m SD.

Typically, males travel longer distances in pursuit of extra pair copulations in areas where potential mates are in low density due to fragmented landscapes (Norris and Stutchbury 2001). Mountain bluebirds nest in cavities in wooded areas or nest boxes erected on fence lines adjacent to large areas of open agricultural fields or grasslands (Johnson and Dawson 2020). As such, travel across these large open spaces is relatively easy as most of these spaces are undefended by bluebirds, making it easier and necessary for individuals to travel considerable distances to seek out extra-pair mates (Balenger et al. 2009b). The long distances between the focal nest and the nest of the extra-pair males in our study are likely a result of low nesting densities due to large open spaces and low density of suitable nest sites on the landscape.

Extra-pair paternity is often linked to physical characteristics as these may be indicators of mate condition or quality (Hutchinson and Griffith 2008; Valcu et al. 2023); however, neither male nor female body size predicted the occurrence of extra-pair paternity. We did observe that all (14/14) extra-pair offspring in the nests of second year (SY) males and 75% (24/32) of extra-pair offspring in the nests of after second year males were sired by after second year (ASY) males. In our study, SY males sired 25% of the extra-pair offspring we were able to assign, and all of those offspring were in the nests of ASY males. This finding is consistent with previous work demonstrating female preference for older males (Jacobs et al. 2015), as age is often linked to differences in plumage (Richardson and Burke 1999; Arct et al 2022), song (Hasselquist et al. 1996; Benitez et al. 2022), and parental care (Snyder and Smallwood 2023).

Mountain bluebirds with more colourful UV-blue plumage are less likely to lose paternity and more likely to gain extra-pair fertilizations (Balenger et al. 2009a). Thus, though we did not find any measures of body size associated with paternity, it is certainly possible that extra-pair paternity is linked to colouration in our population. Future work that integrates measures of UV-blue colouration may help tease apart the relative importance of neighbour proximity/abundance and colouration in female choice of extra-pair mates.

Previous work on our study system demonstrated that tree swallow (*Tachycineta bicolor*) proximity and abundance is associated with reproductive success, though the effects differed depending on the stage of nesting. Early in the season, mountain bluebirds with more tree swallow neighbours within 500m had reduced hatching success, while later in the season a higher abundance of tree swallow neighbours was associated with higher fledging success.

Because sexual interference and aggressive interactions can occur between heterospecific neighbours particularly for nest sites and other resources (Ley et al. 1997; Grether et al. 2017), we tested if interference from tree swallow neighbours could reduce the probability of extra-pair paternity. However, our models showed no effects of tree swallow neighbours on mountain bluebird paternity. Because mountain bluebirds begin nesting ~14 days earlier than tree swallows, their interactions are likely limited during the fertile period for mountain bluebirds.

Consistent with previous research, our work demonstrates that extra-pair paternity tends to increase with increasing density. However, our research illustrates the importance of studying the effects of neighbours at varying spatial scales. While having a high abundance of neighbours at a broad scale (i.e., accessible during long-distance forays) may increase opportunities of extra-pair mating, close neighbours may actually inhibit extra-pair paternity through increased mate guarding and territory defense. Expanding our study to incorporate neighbour distances beyond 1000m may provide an even greater understanding of the influence of neighbour abundance on extra-pair paternity, as mountain bluebirds in our population travel long distances (sometimes >3km) in pursuit of extra-pair fertilizations. Though most work on the effects of neighbours tends to focus on the impact of near neighbours (Stewart et al. 2010; Ryder et al. 2012), our work demonstrates that the scale at which behavioural interactions can occur in bluebirds is vast, requiring us to re-examine the scale at which even distant neighbours may impact patterns of mate choice and paternity.

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CHAPTER 4: CONCLUSION

Interactions between neighbours can influence reproductive success and extra-pair paternity of cavity-nesting birds, yet for nearly all species, the relative importance of conspecific and heterospecific neighbour density and proximity has not been studied. This knowledge gap is especially problematic for species that are dependent on artificial nest boxes, where the placement and distribution of boxes may directly impact population trends. The goal of this thesis was to investigate the influence of conspecific and heterospecific neighbour abundance and proximity on the reproductive success (as measured by hatching and fledging success) of mountain bluebirds (*Sialia currucoides*) and tree swallows (*Tachycineta bicolor*) at nest boxes. I also examined the influence of neighbours on the occurrence of extra-pair paternity and proportion of nestlings sired by extra-pair males at mountain bluebird nests.

Influence of neighbours on reproduction

Because both mountain bluebirds and tree swallows are secondary cavity nesters that occupy the same habitat in areas where their ranges overlap, they are often in direct competition for nest sites. To understand the influence of neighbours on reproductive success, I used eight years (2012-2018) of community science data to examine the hatching and fledging rate at mountain bluebird and tree swallow nests. I found that mountain bluebird neighbour abundance had a positive influence on tree swallow hatching success and mountain bluebird fledging success. However, the influence of tree swallow neighbour abundance on bluebird reproductive success shifted from a negative relationship early in the nesting period (hatching rate) to a positive relationship later in the nesting period (fledging rate). This relationship may be explained in part, by the difference in nest start time between bluebirds and tree swallows. At our study site, the average first egg date for mountain bluebirds was May 10 ±13 days while the average first egg date for tree swallows was May 24 ±7 days. The later start by tree swallows increases the likelihood of interruption of incubating female bluebirds by tree swallows seeking a next box. Frequent interruption of incubating females can lead to hatch reduction as the eggs are repeatedly exposed (Webb 1987; Brazil-Boast et al. 2011). The shift from a negative influence by tree swallow neighbour abundance to a positive one later in the nesting stage may result from byproduct nest defense (Winkler 1994; Grabowska-Zhang et al. 2012). Shared nest defense may

also help explain the improved reproductive success we observed at both conspecific and heterospecific nests as bluebird neighbour abundance increased. The observed increase in fledging success as the number of both conspecific and heterospecific neighbours increased may also be an indication of habitat quality. Higher quality habitat can support more nesting birds (Probst and Hayes 1987) than lower quality habitat improving nest success particularly during provisioning of nestlings (Weinberg and Roth 1998).

The distance to the nearest neighbour's nest also influenced reproductive success. Both bluebirds and tree swallows experienced improved reproductive success as the distance to the nearest tree swallow neighbour decreased. Not unlike neighbour abundance later in the nesting period, this relationship may be explained through mutual nest defense and/or habitat quality. However, while bluebirds may benefit from having a tree swallow neighbour in close proximity, increased neighbour abundance resulted in reduced hatching success for bluebirds.

Nest boxes are often placed along fence lines (sometimes on consecutive fence posts) and on trees adjacent to agricultural fields. While it has been suggested that boxes be placed in pairs to reduce competition between bluebirds and tree swallows (Stanback et al. 2019), our research suggests providing more space between boxes, rather than putting them on adjacent posts, which are typically a few metres apart, and distributing boxes in lower densities on the landscape. Together these practices can improve reproductive success for both species by reducing the negative impact of frequent interference while maintaining the benefit of mutual neighbour nest defense.

An analysis of habitat quality and resource availability would allow us to better understand habitat utilization, and intra- and inter-specific interactions of nesting bluebirds and tree swallows in our study area. We did not examine reproductive output at natural cavities in this study as most of the wooded areas where natural cavities would occur were on private land. While there were certainly pairs nesting in natural cavities in our study area, we observed very few individuals in the area that could not be attributed to a nest box (based on the lack of colour bands). However, information on the location of, and the reproductive success at natural cavities would provide us with a greater understanding of the bluebird and tree swallow community.

Influence of neighbours on extra-pair paternity

Conspecific neighbour abundance and proximity influenced extra-pair paternity at mountain bluebird nests. An increase in neighbour density translates into an increase in the opportunity for extra-pair copulations (Arrieta et al 2022; Di Lecce et al. 2023). I observed a similar trend in my study whereby extra-pair paternity increased as neighbour abundance increased at distances greater than 500m. However, as the abundance of neighbours within 250m increased, extra-pair paternity events decreased. Mountain bluebirds will defend their nest and mate from conspecific intruders (Johnson and Dawson 2020). With an increase in nearby neighbour abundance, bluebirds may increase mate guarding in an attempt to prevent extra-pair copulations and decrease loss of paternity (Dickinson and Leonard 1996).

Individuals will travel long distances in search of extra-pair copulations--extra-pair offspring are often not sired by the nearest neighbour (Charmantier and Perret 2003; Balenger et al. 2009b). Through DNA analysis and paternity assignment, we found that for bluebirds in our study, there was an average of 2199m ± 1357.4m between the nest containing the extra-pair nestling and the nest of the male assigned to that nestling. Based on the distance individuals travel in search of extra-pair copulations, extension of distances to include the number of neighbour nests within 3000m in combination with radio telemetry or other tracking techniques, could shed more light on extra-pair paternity dynamics at our study site.

Colouration is often linked to extra-pair paternity in sexually dimorphic birds (Thibault et al. 2018; Valcu et al 2023). Mountain bluebirds are sexually dimorphic with males displaying a bright blue plumage and younger SY males less brightly coloured than older ASY males. Other studies have shown that more brightly coloured males sire more offspring than less brightly coloured males (Balenger et al 2009a). Future work should integrate a colour analysis of feathers collected from adult bluebirds in our study site to improve our understanding of colouration as a driver of mountain bluebird extra-pair paternity. Lastly, while my thesis focused on extra-pair paternity in mountain bluebirds, future work should investigate the influence of neighbours on extra-pair paternity of tree swallows. Extra-pair paternity is common in tree swallows, with greater than 50% of broods having extra-pair offspring (Barber et al. 1996; Lombardo et al. 2020); however, whether the density and proximity of conspecific and heterospecific neighbours directly impacts extra-pair paternity in our system remains unknown.

The influence of neighbours on reproductive success varies by species and on spatial and temporal scales. Timing of nesting activities can be just as influential as the distribution and abundance of neighbours on reproductive success. Neighbour abundance also influences the occurrence of extra-pair paternity as individuals will travel considerable distance in pursuit of extra-pair copulations. The addition of nest boxes on the landscape provides mountain bluebirds, tree swallows, and other species with precious nest sites as natural cavities become increasingly scarce due to habitat loss from human activity and climate change. Knowledge gained from this study may help guide the placement of nest boxes to maximize reproductive success.

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APPENDIX A
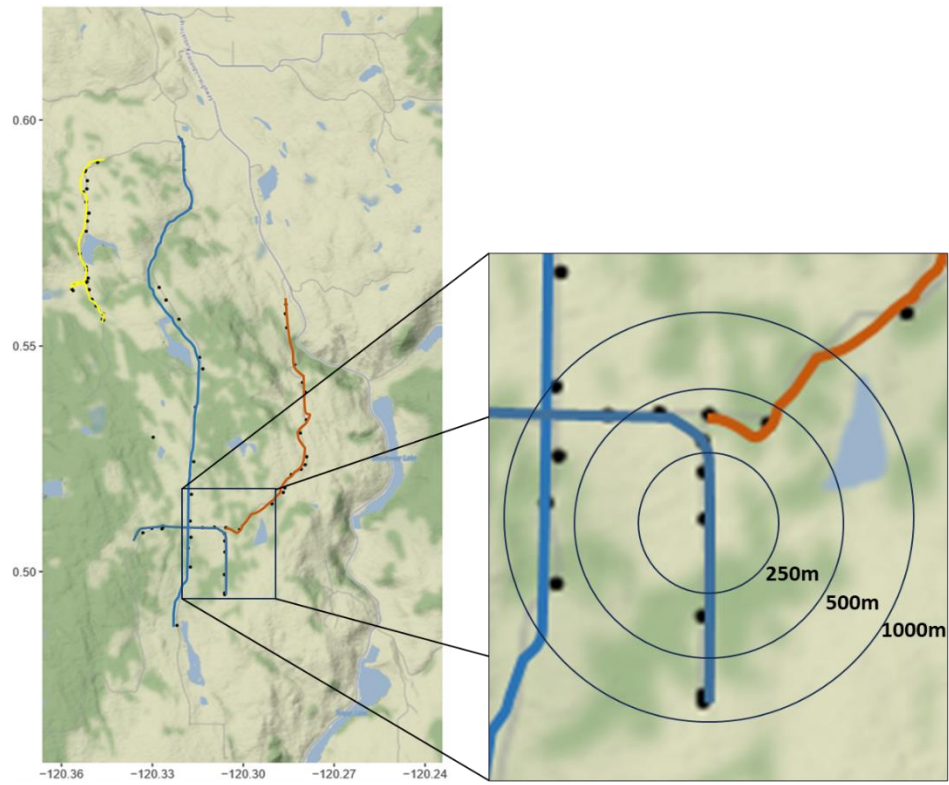
Appendix Figure A.1. Map of three nest box routes south of Kamloops, British Columbia. Example of distance intervals (250m, 500m and 1000m) used to determine neighbour abundance around focal nest (nest box location marked with a black dot).
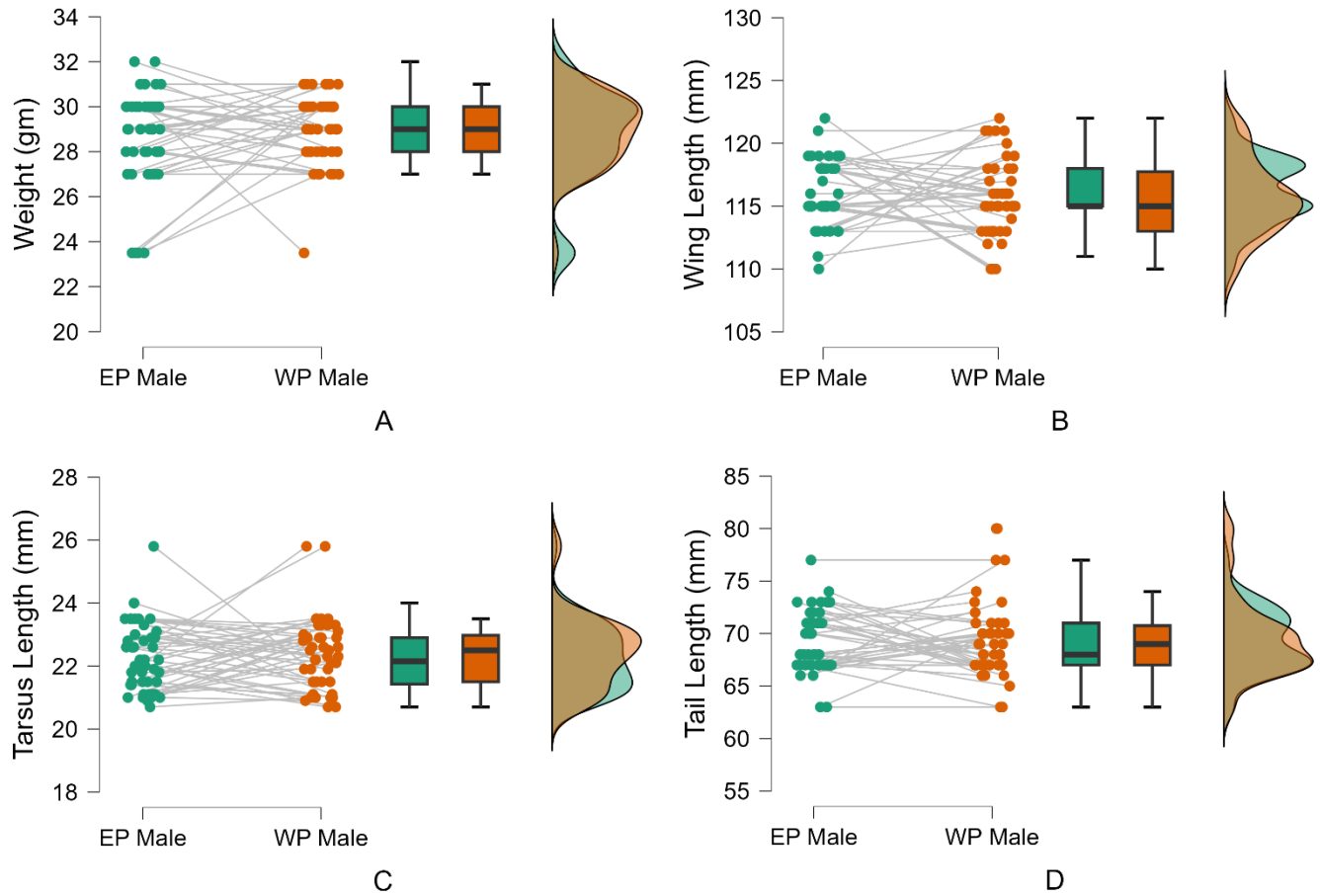
APPENDIX B

Appendix Table B.1. Distance (m) to the nearest conspecific and heterospecific nest for each active mountain bluebird (n = 469) and tree swallow (n = 637) nest observed on 11 nest box routes from 2012 to 2019.

	Nearest MOBL neighbour		Nearest TRES neighbour	
	MOBL	TRES	MOBL	TRES
Mean	456.281	1059.918	625.999	296.972
Std. Error	20.803	72.008	39.453	15.268
Std. Deviation	450.512	1817.398	842.404	385.356
Minimum	3.090	3.090	3.090	6.650
Maximum	3373.850	7773.040	4814.270	2808.620

Appendix Table B.2. Conspecific and heterospecific nest box neighbour abundance at intervals of 250m and 500m from focal mountain bluebird and tree swallow nests.

	TRES 250m		MOBL 250m		TRES 500m		MOBL 500m	
	MOBL	TRES	MOBL	TRES	MOBL	TRES	MOBL	TRES
Mean	0.817	1.636	0.554	0.673	1.667	3.576	1.512	1.414
Std Error	0.050	0.074	0.042	0.035	0.086	0.123	0.069	0.057
Std Dev	1.088	1.868	0.903	0.894	1.855	3.093	1.493	1.430
Minimum	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Maximum	6.000	8.000	5.000	5.000	8.000	13.000	7.000	8.000

APPENDIX C

Appendix Figure C.1. Comparison of weight (A), wing length (B), tarsus length (C), and tail length (D) between the within-pair male (WP Male) and the extra-pair male (EP Male) assigned to the extra-pair offspring in the within-pair male's nest (n=43).