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Effects of urbanization and nest-box design on reproduction vary by species in three cavity-nesting passerines in the Okanagan Valley, British Columbia, Canada

C.A. Dale, M.W. Reudink, L.M. Ratcliffe, and A.E. McKellar

Abstract: Artificial nest boxes provide an important resource for secondary cavity-nesting passerines, whose populations may be limited by the availability of nesting sites. However, previous studies have demonstrated that the design and placement of boxes may affect the reproductive success of the birds that use them. In this study, we asked whether the habitat surrounding a nest box or the type of box influenced reproduction in three cavity-nesting passerines. We studied Western Bluebirds (*Sialia mexicana* Swainson, 1832), Mountain Bluebirds (*Sialia currucoides* (Bechstein, 1798)), and Tree Swallows (*Tachycineta bicolor* (Vieillot, 1808)) breeding in artificial nest boxes at sites across 70 km of the Okanagan Valley of British Columbia, Canada. Sites varied in their degree of urbanization, from relatively undisturbed ranchland, to cultivated vineyards, to frequently disturbed "suburban" habitat, and boxes varied in type of entrance (slot or hole). Western Bluebirds nested earlier in vineyards, and Tree Swallows produced significantly fewer fledglings in suburban habitat. In addition, Tree Swallows nested earlier and produced more fledglings in slot boxes. Our results suggest that conservation actions for cavity-nesting passerines may depend on the target species, which in turn should dictate the appropriate box type and habitat when erecting or replacing nest boxes.

Key words: Western Bluebird, *Sialia mexicana*, Mountain Bluebird, *Sialia currucoides*, Tree Swallow, *Tachycineta bicolor*, reproductive success, nest box, cavity-nesting birds.

Résumé : Les nichoirs artificiels constituent une importante ressource pour les passereaux nichant dans des cavités secondaires, dont les populations pourraient être limitées par la disponibilité de sites de nidification. Des études passées ont toutefois démontré que la conception et l'emplacement des nichoirs ont une incidence sur le succès de reproduction des oiseaux qui les utilisent. Nous avons tenté de déterminer si l'habitat qui entoure un nichoir et le type de nichoir influencent la reproduction de trois passereaux nichant dans des cavités. Nous avons étudié des merlebleus de l'Ouest (*Sialia mexicana* Swainson, 1832), des merlebleus azurés (*Sialia currucoides* (Bechstein, 1798)) et des hirondelles bicolores (*Tachycineta bicolor* (Vieillot, 1808)) qui nidifient dans des nichoirs artificiels dans différents sites répartis sur 70 km de la vallée de l'Okanagan, en Colombie-Britannique (Canada). Les sites différaient sur le plan du degré d'urbanisation, allant de terres d'élevage relativement peu perturbées à des vignobles en culture, à des habitats « suburbains » fréquemment perturbés, et le type d'entrée des nichoirs variait (fente ou trou). Les merlebleus de l'Ouest nidifiaient plus tôt dans les vignobles, et les hirondelles bicolores produisaient significativement moins de jeunes à l'envol dans les habitats suburbains. En outre, les hirondelles bicolores nidifiaient plus tôt et produisaient plus de jeunes à l'envol dans les nichoirs à fente. Nos résultats donnent à penser que les meilleures mesures de conservation pour les passereaux nichant dans des cavités pourraient dépendre de l'espèce, ce qui devrait en retour dicter les bons types de nichoir et d'habitat au moment d'aménager ou de remplacer des nichoirs. [Traduit par la Rédaction]

Mots-clés : merlebleu de l'Ouest, *Sialia mexicana*, merlebleu azuré, *Sialia currucoides*, hirondelle bicolore, *Tachycineta bicolor*, succès de reproduction, nichoir, oiseaux nichant dans des cavités.

Introduction

Secondary cavity-nesting birds do not excavate their own nest sites, instead relying on naturally occurring cavities. Consequently, their populations are often limited by the availability of suitable nesting sites, particularly in managed forests, where trees are often logged before becoming old enough to house cavities, and decaying snags are typically removed (Newton 1994). Thus, decreases in cavity availability due to human activities may contribute to population declines in obligate secondary cavity-nesting species (Copley et al. 1999; Wetzel and Krupa 2013).

The provision of artificial cavities (usually nest boxes) may overcome the limitation of nest site availability and lead to increases in population size and breeding density of cavity-nesting species (Holroyd 1975; Brawn and Balda 1988; Newton 1994; Aitken and Martin 2012). As a result, nest boxes are often established as part of management strategies for declining cavity nesters (e.g., Copley et al. 1999; Zingg et al. 2010). In some cases, such as the bluebirds

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Fig. 1. Box types available to secondary cavity nesters in the Okanagan Valley of British Columbia, Canada: (A) hole box; (B) slot box. Colour version online.

(genus *Sialia* Swainson, 1827) of North America (Backhouse 1986) and the British Columbia population of Purple Martins (*Progne subis* (Linnaeus, 1758)) (Copley et al. 1999), successful reversal of population declines has been partly credited to the widespread establishment of nest-box programs. However, a growing body of evidence indicates the placement and the design of nest boxes strongly influence their effectiveness in a wide variety of cavity-nesting species.

Because habitat is often a key determinant of reproductive success in birds, it is not surprising that the habitat in which nest boxes are erected may affect the timing and success of breeding for secondary cavity nesters. For example, European Pied Flycatcher (*Ficedula hypoleuca* (Pallas, 1764)) pairs nesting in boxes in deciduous forest have been shown to lay eggs earlier and have greater reproductive success than those nesting in boxes in coniferous forest (Lundberg et al. 1981; Huhta et al. 1998). Even within deciduous forests, their reproductive success varied with the proportion of mature trees versus saplings, the tree species present, and the proximity of the nest box to water (Goodenough 2014).

In addition, nest boxes are often erected in habitat that has been influenced by anthropogenic activities, such as land-use change, urbanization, and increased human disturbance, all of which may influence the nesting phenology and success of box nesters. In Tree Swallows (*Tachycineta bicolor* (Vieillot, 1808)), both adult and nestling body condition were lower in birds breeding in nest boxes within agricultural sites than in those breeding in boxes erected in grassland (Michelson et al. 2018), and intensive agriculture has been associated with reduced reproductive success (Rioux Paquette et al. 2014). Great Tits (*Parus major* Linnaeus, 1758) breeding in boxes in urban habitats were shown to have earlier laying dates but lower reproductive success than those breeding in boxes in rural habitats (de Satgé et al. 2019). Even in rural or suburban habitats, human activity may negatively affect cavity nesters in close proximity to roads (Kuitunen et al. 2003) and footpaths (Goodenough 2014), or subjected to other forms of human disturbance (Strasser and Heath 2013). However, the effect of human disturbance is not always negative: Eastern Bluebird (*Sialia sialis* (Linnaeus, 1758)) reproductive success has been shown to peak at intermediate disturbance levels, suggesting this species may be pre-adapted to anthropogenic disturbance, perhaps as a result of intense selection to breed in artificial cavities (Kight and Swaddle 2007). Alternatively, intermediate disturbance areas may provide some advantages to generalist species like Eastern Bluebirds, such as diverse habitat or input of water and (or) nutrients from anthropogenic activities.

In addition to habitat, a wealth of evidence indicates that the characteristics of nest boxes can influence the success of the birds using them (Lambrechts et al. 2010). The material used to construct boxes can affect nest microclimate and vulnerability to predators and parasites, which may in turn influence the timing and success of breeding attempts (e.g., García-Navas et al. 2008; Bueno-Enciso et al. 2016). Box size can also affect reproduction: for example, Eurasian Wrynecks (*Jynx torquilla* Linnaeus, 1758) in Switzerland preferentially nested in smaller boxes and produced heavier nestlings in those boxes (Zingg et al. 2010), whereas House Sparrows (*Passer domesticus* (Linnaeus, 1758)) in Illinois, USA, produced smaller clutches in smaller boxes (Lowther 2012). Finally, box design can matter as well; in Wisconsin, Eastern Bluebirds nesting in open-top boxes were more successful than those nesting in standard, rectangular boxes with covered roofs (Radunzel et al. 1997). Even the shape of the box opening can affect reproductive success: in British Columbia, Mountain Bluebirds (*Sialia currucoides* (Bechstein, 1798)) had higher fledging success in boxes with hole-shaped entrances than in boxes with slot-shaped entrances, possibly because hole-shaped entrances provide increased protection against predation and inclement weather (Leroux et al. 2018).

Understanding the effects of habitat and nest-box design is important because variation in boxes can make it challenging to compare results across different studies (Lambrechts et al. 2010). In addition, nest-box programs aimed at conservation that fail to consider these factors may do more harm than good. Poorly placed or designed nest boxes can create ecological traps, which are common in human-altered environments and occur when habitat attractiveness becomes decoupled from habitat quality (Schlaepfer et al. 2002; Mänd et al. 2005; Rodríguez et al. 2011).

In this study, we asked whether the habitat in which nest boxes were placed or the type of entrance affected the reproductive success of three species of secondary cavity nesters breeding in the Okanagan Valley of British Columbia, Canada: Western Bluebirds (*Sialia mexicana* Swainson, 1832), Mountain Bluebirds, and Tree Swallows. The habitats we investigated varied along a continuum of human disturbance, from ranchlands (rarely disturbed) to suburban habitats (frequently disturbed), and box entrances were either hole- or slot-shaped. While a number of studies have examined the effect of nest-box placement and design on reproductive success in secondary cavity nesters, this study is among the first to consider multiple species concurrently across multiple habitat types varying in amount of human disturbance, which allows us to determine whether these effects are generalizable or differ across species.

Table 1. Number of available boxes with hole- or slot-shaped entrances across three different habitat types in 2011 and 2012.

	Hole boxes		Slot boxes	
	2011	2012	2011	2012
Ranchland	1 (0)	1 (0)	42 (21)	39 (8)
Suburban	0 (0)	0 (0)	52 (12)	57 (13)
Vineyard	162 (70)	161 (73)	68 (43)	91 (42)

Note: Values in parentheses indicate the number of boxes of each type remaining unoccupied by any species in each year.

Table 2. Sample sizes of Western Bluebird (*Sialia mexicana*), Mountain Bluebird (*Sialia currucoides*), and Tree Swallow (*Tachycineta bicolor*) nests in boxes with hole- or slot-shaped entrances across three different habitats.

	Habitat type	Hole boxes	Slot boxes	Total
Western Bluebird	Ranchland	1	27	28
	Suburban	0	41	41
	Vineyard	73	24	97
Mountain Bluebird	Ranchland	1	4	5
	Suburban	0	0	0
	Vineyard	7	1	8
Tree Swallow	Ranchland	1	2	3
	Suburban	0	13	13
	Vineyard	33	18	51

We predicted that Tree Swallow reproductive success would be lowest in vineyard boxes, as previous studies have shown a negative effect of agriculture on body condition and number of fledglings in Tree Swallows (Rioux Paquette et al. 2014; Michelson et al. 2018). In contrast, we expected Mountain Bluebirds and Western Bluebirds to have the highest reproductive success at the intermediate levels of disturbance found in vineyards, as has been found for closely related Eastern Bluebirds (Kight and Swaddle 2007). However, we predicted that reproductive success would be higher in boxes with hole-shaped entrances than those with slot-shaped entrances for all three species, as protection against predation and inclement weather should benefit all cavity nesters.

Materials and methods

Field methods

Mountain Bluebirds, Western Bluebirds, and Tree Swallows are all obligate secondary cavity nesters. They are common breeders in interior British Columbia and begin laying eggs as early as 29 March, 10 April, and 16 April, respectively (Campbell et al. 1997*a*, 1997*b*, 1997*c*). Mountain Bluebirds and Western Bluebirds in British Columbia may produce multiple broods in one breeding season (Guinan et al. 2008; Johnson and Dawson 2019); however, while Tree Swallows may replace broods lost to predation early in the breeding season, they rarely re-nest following a successful breeding attempt (Winkler et al. 2011).

Data for this study were collected in the Okanagan Valley from April to August of 2011 and 2012. We monitored approximately 350 boxes at 10 sites stretching across 70 km of the southern Okanagan (from 49°33′N to 49°05′N). Boxes were located in three different types of habitat: ranchland boxes were on undeveloped land used primarily for cattle grazing, vineyard boxes were on working vineyards, and suburban boxes were along walking trails, in backyards, or on roadsides. Vineyard and suburban sites were usually within a few hundred metres of areas of natural habitat, and vineyard sites ranged in size from approximately 18 to 75 ha. Vineyard boxes were typically mounted on fenceposts around the edges of the site; however, in several cases, boxes were also distributed throughout the interior of the vineyard. Habitat type corresponded strongly with nest-box-specific disturbance scores collected at a subset of the boxes used in our study (see Bhardwaj et al. 2015). Suburban habitats experienced the greatest amount of human disturbance, followed by vineyards (intermediate), and ranchland. Boxes varied in the shape of the opening, so for each box, we noted whether the opening was a round hole (Fig. 1A) or a rectangular slot (Fig. 1B).

Most boxes used had been erected prior to the study by local Bluebird enthusiasts, which allowed us to work with established populations of secondary cavity nesters; however, as a result, box types were not distributed evenly across habitats, and hole boxes were almost entirely restricted to vineyard habitat (Table 1). Number of available boxes varied slightly across the years of the study because several boxes fell down or were destroyed, while some new boxes were installed and one vineyard site was monitored only in 2012. Only 25 new boxes (all with slot-shaped entrances) were installed for this study: 10 in ranchland, 5 in suburban habitat, and 10 in vineyards.

Beginning in mid-March each year, we checked boxes every 3–4 days and recorded their contents. In both years, roughly a third of the boxes remained unoccupied (Table 1). Occupied boxes were used by 11 different species, but for 6 of those species, we found fewer than five nests. Western Bluebirds were the most common species occupying boxes, followed by Tree Swallows, House Wrens (*Troglodytes aedon* Vieillot, 1809), Mountain Bluebirds, and House Sparrows, respectively. We chose to focus our study on Western Bluebirds and Tree Swallows because they were the species most frequently found in boxes; we included Mountain Bluebirds to allow us to compare our findings with those of Leroux et al. 2018.

For the three focal species, box checks were conducted more frequently (1–2 days) around estimated hatching and fledging dates to determine exact dates where possible. When nests contained partial clutches, first egg dates were calculated by backdating, assuming females laid one egg per day (Guinan et al. 2008; Winkler et al. 2011; Johnson and Dawson 2019).

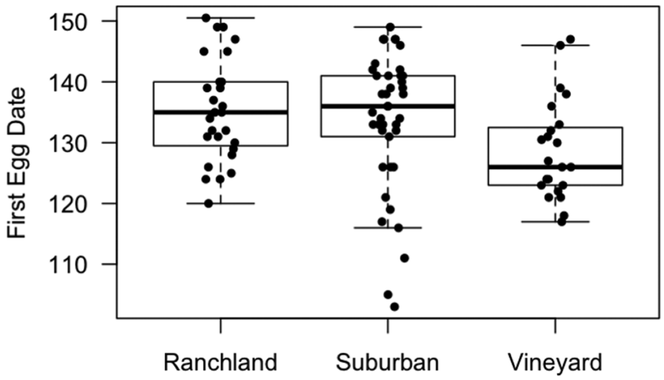
Data analysis

We restricted our data to include only first nesting attempts. Based on the upper bound of the 95% confidence interval of first egg dates from known Western Bluebird first attempts, Bluebird nests with first egg dates after an ordinal date of 152 (1 June in 2011; 31 May in 2012) were excluded from the analysis. For Tree Swallows, there was a clear bimodal distribution of first-egg dates, with late dates likely indicative of re-nesting after a failed nest attempt. As such, nests with first egg dates after an ordinal date of 160 were excluded from our analysis.

We asked whether nesting habitat (suburban, vineyard, ranchland) and nest-box type (hole entrance, slot entrance) influenced the timing or success of reproduction (first egg date, number of eggs, number of fledglings, and proportion of young fledged (fledglings/eggs)) in Western Bluebirds, Mountain Bluebirds, and Tree Swallows. For reproductive timing, we constructed a linear mixed model with first egg date as a response variable, habitat or box as a fixed effect, and year as a random effect. For reproductive success, we constructed a series of generalized linear mixed models using each reproductive variable as a response with Poisson (for number of eggs and fledglings) or binomial (for proportion of young fledged) error distributions, habitat or box type as fixed effects, and year as a random effect. Due to an unbalanced distribution of habitat and box-type occupancy across species, these models were modified for each species.

Western Bluebird nests were present across all three habitat types; however, the proportion of Western Bluebirds nesting in hole and slot boxes varied across habitats (Table 2). As such, we were unable to include both habitat and box type in the same model for Western Bluebirds. To assess the role of habitat on

Fig. 2. Western Bluebirds (*Sialia mexicana*) in vineyard habitats had significantly earlier first egg dates than birds nesting in either ranchland or suburban habitat.



reproduction, we restricted our dataset to the box type distributed across all habitats (slot boxes), then created a model using only habitat as a main effect. Next, to assess the role of box type, we restricted our dataset to the habitat containing both box types (vineyards) and created a model using only box type as a main effect.

Mountain Bluebird nests were observed only in vineyard and ranchland habitats. Again, the proportion of birds occupying hole and slot boxes differed across habitats (Table 2). Because habitat and box type were highly confounded, we again created two separate models, one that only included habitat as a main effect and one that only included box type as a main effect, with the understanding that for any significant effects, we would be unlikely to be able to differentiate between potential influences of habitat versus box type.

Tree Swallows occupied nest boxes in each habitat type; however, due to the small sample size of nests in ranchland (Table 2), we were only able to compare vineyard and suburban habitats and restricted our analysis to the box type found in both habitats (slot boxes). To assess the effect of box type on reproductive success, we restricted our dataset to the habitat containing both box types (vineyards) and created a model using only box type as a main effect.

Ethical note

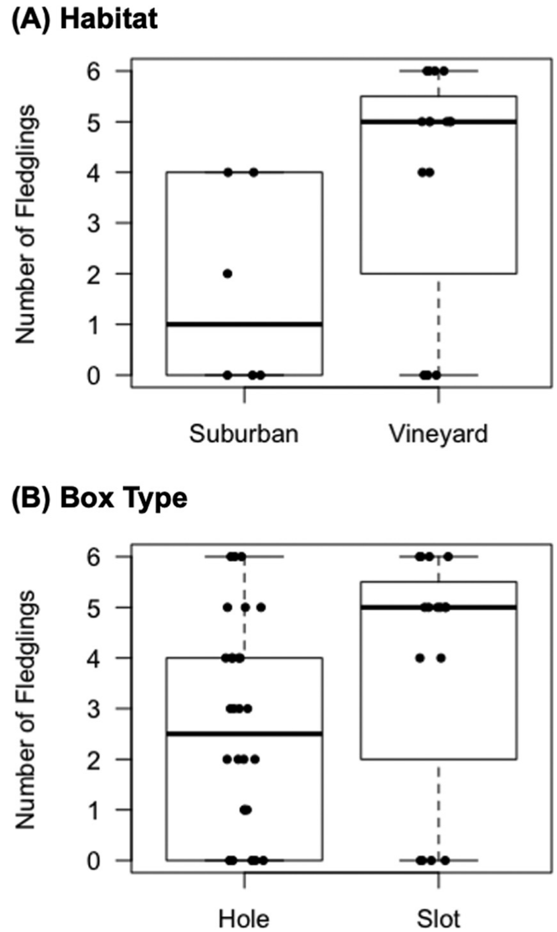
This study followed the guidelines established by the Canadian Council on Animal Care (CCAC). All work complied with Canadian laws and was performed in accordance with permits issued by the Queen's University Animal Care Committee (Ratcliffe-2010-046), Canadian Wildlife Services (banding permit 10829 and collection permit BC-11-0001), and BC Parks (use permit 104985).

Results

Western Bluebirds

When we examined the effect of habitat on reproduction for Western Bluebirds nesting in slot boxes, birds nesting in vineyard habitat had significantly earlier first egg dates (day 128.63 ± 8.21 (mean ± SD)) than birds nesting in suburban (day 133.61 ± 11.33) and ranchland habitat (day 135.28 ± 8.48) ($\chi^2_{[1]}$ = 6.35, p = 0.04; Fig. 2). We found no differences in number of eggs ($\chi^2_{[2]}$ = 0.49, p = 0.78), number of fledglings ($\chi^2_{[2]}$ = 0.27, p = 0.88), or proportion fledged ($\chi^2_{[2]}$ = 0.00, p = 0.99). When we examined the effect of box type on reproductive timing and success for pairs nesting in vineyard habitat, we found no difference in first egg date ($\chi^2_{[1]}$ = 0.17, p = 0.68), number of eggs ($\chi^2_{[1]}$ = 0.24, p = 0.63), number of fledglings ($\chi^2_{[1]}$ = 0.01, p = 0.90), or proportion fledged ($\chi^2_{[1]}$ = 0.40, p = 0.53) between hole and slot boxes.

Fig. 3. (A) Tree Swallows (*Tachycineta bicolor*) nesting in slot boxes in vineyard habitat fledged significantly more offspring than Tree Swallows nesting in slot boxes in suburban habitat. (B) Tree Swallows nesting in vineyard habitat fledged significantly more offspring when nesting in slot boxes than in hole boxes.



Mountain Bluebirds

For Mountain Bluebirds, first egg dates were earlier in vineyard habitat (day 122.75 ± 3.75 (mean ± SD)) than ranchland habitat (day 137.80 ± 4.74) ($\chi^2_{[1]}$ = 7.34, p = 0.007). Similarly, first egg dates were earlier in hole boxes (day 120.50 ± 2.58) than slot boxes (day 141.40 ± 3.27) ($\chi^2_{[1]}$ = 39.20, $p < 0.0001$). Given that nearly all (4/5) Mountain Bluebird nests in ranchland occurred in boxes with slot entrances, and nearly all (7/8) nests in vineyard occurred in boxes with hole entrances (Table 2), it is unclear whether the above patterns are being driven by habitat or box type. We found no effects of habitat on the number of eggs ($\chi^2_{[1]}$ = 0.01, p = 0.92), number of fledglings ($\chi^2_{[1]}$ = 0.00, p = 0.98), or proportion fledged ($\chi^2_{[1]}$ = 0.00, p = 0.96). Similarly, we found no effect of box type on the number of eggs ($\chi^2_{[1]}$ = 0.01, p = 0.92), number of fledglings ($\chi^2_{[1]}$ = 2.27, p = 0.13), or proportion of offspring fledged ($\chi^2_{[1]}$ = 1.27, p = 0.26).

Tree Swallows

When we examined differences in Tree Swallow reproductive timing and success between habitats (vineyard versus suburban), we found no difference in first egg dates ($\chi^2_{[1]}$ = 0.57, p = 0.45) or number of eggs ($\chi^2_{[1]}$ = 0.35, p = 0.55), but Tree Swallows nesting in vineyard habitat fledged a greater number of young ($\chi^2_{[1]}$ = 6.12, p = 0.01; suburban: 1.67 ± 1.97 (mean ± SD); vineyard: 2.94 ± 2.28; Fig. 3A), and there was a marginal but non-significant difference in the proportion of young fledged, with a greater proportion of young fledging in vineyard habitat ($\chi^2_{[1]}$ = 3.38, p = 0.07).

When we examined the effect of box type on reproduction for pairs nesting in vineyard habitat, we found that birds nesting in slot boxes had earlier first egg dates (day 144.77 ± 4.21 (mean ± SD) than those in hole boxes (day 147.48 ± 3.89) ($\chi^2_{[1]}$ = 4.02, p = 0.045). We found no effect of box type on number of eggs ($\chi^2_{[1]}$ = 0.71, p = 0.40). However, there was a significant effect of box type on number of fledglings ($\chi^2_{[1]}$ = 6.17, p = 0.01; Fig. 3B): Tree Swallows nesting in slot boxes produced more fledglings (3.41 ± 2.28 (mean ± SD)) than birds in hole boxes (2.45 ± 2.10). There was also a marginal but non-significant difference in the proportion of young fledged between box types, with a greater proportion of young fledging in slot boxes ($\chi^2_{[1]}$ = 2.81, p = 0.09).

Discussion

In this study, we asked whether habitat or nest-box design were related to variation in reproductive timing and success in three species of secondary cavity nesters. Our findings differed across the three species, but they were largely contrary to our predictions. Reproductive success did not vary across habitats for Western Bluebirds and Mountain Bluebirds; however, both species had earlier first egg dates in vineyard habitats. Tree Swallows did not differ in reproductive timing across habitats, but fledged more young in vineyard habitat than in suburban habitat. Similarly, reproductive success did not differ between box types for either Bluebird species, but Mountain Bluebirds had earlier first egg dates in hole boxes. However, it is important to note that almost all boxes used by Mountain Bluebirds in vineyard habitat had hole entrances, making it impossible to differentiate between the effects of habitat and box type in this species. Tree Swallows had earlier first egg dates and fledged more young in boxes with a slot opening than those with a hole opening.

Interspecific variation in the relationship between reproductive success and box placement and design comes as no surprise. There is ample evidence from previous studies that nest-box preferences and effects differ across cavity-nesting species. For example, Eurasian Tree Sparrows (*Passer montanus* (Linnaeus, 1758)) have higher reproductive success in woodcrete boxes than in wood boxes (García-Navas et al. 2008), but the opposite is true for Blue Tits (*Cyanistes caeruleus* (Linnaeus, 1758)) and Great Tits (Bueno-Enciso et al. 2016). Differences in "ideal" box location and design likely arise as a result of variation in size, foraging strategies, phenology, and life-history traits across secondary cavity-nesting species.

Habitat affected timing of breeding in Western Bluebirds (and potentially Mountain Bluebirds): females laid eggs earlier in vineyards than in ranchland or suburban habitat. These differences in reproductive timing are consistent with Fiehler et al. (2006), who found Western Bluebirds breeding in boxes on vineyards had earlier clutch initiation dates and laid larger clutches than those breeding in native oak–savannah habitat. Variation in timing of egg laying may be related to differences in food availability across habitats; Fiehler et al. (2006) suggest that the predictable water supply provided by vineyard irrigation may increase the size of the insect population and thus the food supply for insectivorous birds. Earlier breeding is often associated with higher reproductive success and may be particularly advantageous for species such as Western Bluebirds that often produce multiple broods in a season (e.g., Townsend et al. 2013).

In contrast to several studies showing negative effects of anthropogenic activity on the reproductive success of box-nesting birds (e.g., Kuitunen et al. 2003; Goodenough 2014; de Satgé et al. 2019), we found no difference in reproductive success across habitats experiencing varying levels of anthropogenic disturbance for either Bluebird species. One possible explanation for the lack of variation in reproductive success across habitats is that Bluebirds are more tolerant of anthropogenic disturbance than many other box-nesting species. A number of studies support this hypothesis: Kight and Swaddle (2007) found that Eastern Bluebirds had the highest reproductive success at intermediate levels of anthropogenic disturbance; Stanback and Seifert (2005) found no difference in brood size between Eastern Bluebirds nesting in boxes on and off golf courses; and Leclerc et al. (2005) found that pairs nesting on golf courses actually produced more young than those nesting in more natural areas. Taken together, these studies suggest that *Sialia* species might be relatively tolerant of human disturbance. Although this does not preclude negative effects at very high disturbance levels, as observed in Eastern Bluebirds (Kight and Swaddle 2007), we found no evidence supporting our prediction that Bluebird reproductive success would peak at intermediate levels.

We did detect an effect of habitat on reproductive success in Tree Swallows: contrary to our predictions, pairs nesting in vineyard boxes fledged more young than those in nesting in suburban boxes. Although previous studies suggest that Tree Swallows are negatively affected by agriculture (Ghilain and Bélisle 2008; Rioux Paquette et al. 2014; Michelson et al. 2018), they may also be impacted by several characteristics of anthropogenically disturbed habitats, such as increased noise from traffic (Injaian et al. 2018) and exposure to polycyclic aromatic compounds, which are found in vehicle emissions (Fernie et al. 2018). However, there is no clear reason why these factors would have affected Tree Swallows but not the two *Sialia* species in our study; indeed, a study of Eastern Bluebirds suggests Bluebird reproductive success is also negatively impacted by noisy environments (Kight et al. 2012).

Foraging behaviour is one of the key differences between Tree Swallows and the two Bluebird species: Tree Swallows are aerial insectivores (Winkler et al. 2011), whereas Western Bluebirds and Mountain Bluebirds are mainly perch-foragers (Guinan et al. 2008; Johnson and Dawson 2019). It is possible that Tree Swallow reproductive success was lower in suburban habitats due to decreased food availability. However, given that previous studies have shown agriculture is associated with decreases in aerial insect populations (Paquette et al. 2013) and reproductive success in Tree Swallows (Ghilain and Bélisle 2008; Rioux Paquette et al. 2014), we might expect less food to be available in vineyards than suburban areas, rather than vice versa. A direct comparison of food availability between habitats would be necessary to form conclusions about the cause of variation in Tree Swallow reproductive success across habitats.

Contrary to our predictions and a previous study of Mountain Bluebirds (Leroux et al. 2018), we found no effect of box type (i.e., hole or slot entrance) on reproductive success for Western Bluebirds or Mountain Bluebirds. Leroux et al. (2018) suggested that boxes with hole openings might provide additional protection from predators and inclement weather, thus increasing nestling survival. Our conflicting results could be explained if predators and (or) inclement weather posed less risk in the Okanagan, at least during the years of this study, thus negating the advantage of hole boxes. Alternatively, our very small sample size of Mountain Bluebird nests could explain the lack of detectable patterns. Indeed, although the difference was not significant (p = 0.13), Mountain Bluebirds tended to produce more fledglings in hole boxes (4.25 ± 1.28) than in slot boxes (2.6 ± 2.51), similar to the pattern observed by Leroux et al. (2018). However, as habitat and box type were confounded for Mountain Bluebirds in our study, we are unable to disentangle the effects of these two variables.

In contrast, we found that Tree Swallows began breeding earlier and fledged more young in slot boxes than in hole boxes. This was surprising: if hole boxes do reduce exposure to inclement weather and predation, then we would expect all species to have higher reproductive success in these boxes. However, it is possible that the qualities that benefit Mountain Bluebirds in Kamloops, British Columbia, may in fact be detrimental to Tree Swallows in the Okanagan. If hole boxes provide greater protection, then they may also be warmer inside. Given that Tree

Swallows in this study nested roughly 2 weeks later than both Bluebird species and inclement weather may pose less of a threat to breeding in the Okanagan, higher box temperatures could be a liability for Tree Swallows in the Okanagan, and nestlings in hole boxes may experience hyperthermia. In addition, the fact that Tree Swallows nested several days earlier in slot boxes may indicate that early-arriving Swallows preferentially chose slot boxes.

Overall, the results of our study indicate that the relationship between reproductive success and nest-box placement and design varies across species and sites. This, in turn, implies that conservation actions for cavity-nesting passerines will depend on the target species and the site, and the appropriate box type and habitat should be monitored and adjusted over time to maximize the success of conservation efforts. In the absence of species-specific conservation targets, it may be most prudent to maintain a mix of different box types. Given that suburban habitat negatively affected reproductive success in Tree Swallows and impacted reproductive timing in Western Bluebirds, we recommend that new nest-box placement be focused in habitat types other than suburban, high disturbance areas whenever possible. However, we caution that additional research would be needed to determine whether the negative impacts of suburban boxes (e.g., as ecological traps) for these species outweigh the positive impacts of simply having additional nest sites available.

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