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The influence of weather and parental provisioning on fledging success depends on nest box type in a cavity-nesting passerine, the Mountain Bluebird (*Sialia currucoides*)

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ABSTRACT—Both weather and parental care can influence avian reproductive success, yet few studies have investigated these 2 factors simultaneously. Examining these factors under a common framework is informative because they may interact to influence overall productivity; for example, weather could directly influence nestling survival or could act indirectly by influencing rates of provisioning. To tease apart these possibilities, we used piecewise structural equation modeling and path analysis to assess the relative influence of local weather (temperature and rainfall) and rates of provisioning on the fledging success of Mountain Bluebirds (*Sialia currucoides*) breeding in nest boxes. Both ambient temperature during the nestling period and provisioning rates influenced fledging success, but this finding was dependent on nest box entrance type. Bluebirds nesting in boxes with a hole-shaped entrance had higher overall fledging success than those using boxes with a slot-shaped entrance and exhibited a positive association between fledging success and provisioning rates but a negative association with temperature. Bluebirds nesting in boxes with a slot-shaped entrance experienced reduced fledging success, and success was only weakly associated with provisioning rates. Reduced fledging success for birds nesting in slot boxes may be due to increased exposure and higher susceptibility to stochastic events (e.g., storms), which may also mask any effects of parental effort on success rates. Based on these findings, we recommend the use of nest boxes with hole-shaped rather than slot-shaped entrances when managers and conservation groups establish new bluebird routes or replace existing boxes. *Received 7 July 2017. Accepted 27 March 2018.*

Key words: fledging, mountain bluebird, nest box, parental care, provisioning, weather.

L'influence des conditions météorologiques et de l'approvisionnement parentale sur le succès d'envol chez un passereau nicheur cavicole dépend du type de nichoir

RÉSUMÉ (French)—Les conditions météorologiques ainsi que l'approvisionnement parentale peuvent influencer le succès reproducteur aviaire; peu d'études, cependant, ont exploré ces deux facteurs simultanément. L'examen de ces facteurs dans le cadre d'un même programme d'étude est informatif puisque ces facteurs peuvent interagir de façon à influencer la productivité totale; par exemple, les conditions météorologiques pourraient directement influencer la survie des oisillons ou agir indirectement en influençant le taux d'approvisionnement. Pour distinguer ces influences directes et indirectes, nous avons employé une modélisation par équation structurelle séquentielle ainsi que l'analyse des trajectoires, permettant de déterminer l'influence des conditions météorologiques locales (température et précipitation) et de l'approvisionnement sur le succès d'envol de merlebleus azurés (*Sialia currucoides*) utilisant des nichoirs. La température ambiante pendant la période de nidification de même que le taux d'approvisionnement ont influencé le succès d'envol, mais le résultat variait selon le type de nichoir. Les merlebleus utilisant des nichoirs avec trou d'entrée circulaire avaient un succès d'envol plus élevé que ceux utilisant des nichoirs avec trou d'entrée en forme de fente verticale, et le succès d'envol était positivement lié au taux d'approvisionnement mais négativement lié à la température. Les merlebleus utilisant des nichoirs avec entrée en forme de fente avaient un succès d'envol réduit, et le succès d'envol était faiblement lié au taux d'approvisionnement. Le succès d'envol inférieur observé parmi les oiseaux utilisant les nichoirs avec entrée en forme de fente était possiblement dû à une plus grande exposition et sensibilité du nid aux événements stochastiques (e.g. tempêtes), ce qui pourrait également masquer les effets de l'approvisionnement parentale sur le taux de succès d'envol. Compte tenu de ces résultats, nous recommandons de munir les nichoirs d'une entrée circulaire plutôt que d'une entrée en forme de fente verticale lorsque gestionnaires et groupes de conservation cherchent à créer de nouveaux sentiers de nichoirs ou veulent remplacer des nichoirs existants.

Mots-clés: approvisionnement, conditions météorologiques, envol, merlebleu azuré, nichoir, soins parentaux.

Weather conditions during the breeding season can influence avian reproductive success in several ways. For example, extreme temperatures (Pipoly et al. 2013) and rainfall events (George et al. 1992, Grant et al. 2000) can directly influence hatching and fledging success. In addition, weather can indirectly influence reproductive success through habitat changes (e.g., drought conditions; Ludlow et al. 2014) or changes in food availability and abundance (Grant et al. 2000). Weather may also indirectly affect reproductive success through its

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effects on levels of parental care, such as nestling provisioning rates (Siikamäki 1998, Hoset et al. 2004).

Variation in parental investment in the form of provisioning can have a major impact on the reproductive success of individuals in species with altricial young (Wright et al. 1998, Rauter et al. 2000). Increased parental care can improve nestling growth rates (Klug and Bonsall 2014), leading to greater fledgling mass and better overall condition (Lifjeld et al. 1998, Soma et al. 2006, Wilkin et al. 2009). In turn, these factors can increase offspring survival and recruitment (Naef-Daenzer et al. 2001, Monrós et al. 2002).

Because weather can influence levels of parental provisioning, it can thus also influence reproductive success indirectly. For example, in Water Pipits (*Anthus spinoletta*), females increase provisioning rates with decreasing ambient temperature (Rauter et al. 2000), as is true for Snow Buntings (*Plectrophenax nivalis*) breeding in the Arctic (Hoset et al. 2004). The availability of insect prey, which influences the rate at which parents can provision their offspring, can also be mediated by weather conditions (White 2008). Thus, while both weather and provisioning can affect reproductive success, the relative importance of each factor may depend on the species and the weather conditions experienced. In this study, we examined the relative importance of weather and parental provisioning rates for predicting fledging success of a cavity-nesting passerine, the Mountain Bluebird (*Sialia currucoides*).

For cavity-nesting birds that readily accept boxes for nesting, further variation in reproductive success might be introduced by specific characteristics of the box, such as orientation, entrance size, or inner dimensions (Lambrechts et al. 2010). For example, in a long-term study of Great Tits (*Parus major*) breeding in Wytham Woods in the United Kingdom, the implementation of predator-proof nest boxes resulted in marked changes in clutch size, local recruitment, and adult survival (McCleery et al. 1996, Julliard et al. 1997). Nest box design and construction materials often differ geographically for the same study species, but the benefits of such differences (e.g., more insulated boxes in colder environments) or their potential confounding effects on comparisons among populations have rarely been considered (Lambrechts et al. 2010). Even within a single study population, box types might differ, for example if new designs are introduced gradually over time. This is the case at our study site in British Columbia, Canada, where boxes with 2 different entrance types (slot or hole; Fig. 1) are distributed throughout the region.

Previously, we demonstrated that weather conditions were associated with fledging success in Mountain Bluebirds at our study site (McArthur et al. 2017); however, whether this effect acts directly (through nestling mortality) or indirectly (through a reduction in provisioning) remains unknown. In this study, we first asked whether fledging success differed between boxes with the 2 types of entrances. We then used path analyses to examine the relative direct and indirect influences of local weather and level of parental provisioning on fledging success.

Methods

Study species

Mountain Bluebirds are obligate secondary cavity-nesting thrushes that readily breed in nest boxes throughout western North America's grasslands. These birds are migratory and arrive in interior British Columbia in late winter/early spring (late Feb–Mar) before initiating breeding in early May. Predominantly ground-foraging insectivores during the breeding season, their diet at this time consists mostly of Coleoptera, Orthoptera, Formicidae, Lepidoptera, Hymenoptera, and Hemiptera (Power and Lombardo 1996). Mountain Bluebirds are socially monogamous but utilize a mixed mating strategy (Balenger et al. 2007); both males and females provision offspring, but females tend to provision at higher rates, and only females brood (Power and Lombardo 1996). Mountain Bluebirds can sometimes have more than one brood in a season (Power and Lombardo 1996), but multiple broods are relatively infrequent in our population and our analyses only included first clutches.

Field methods

Fieldwork for this project was conducted on bluebird trails maintained by the Kamloops Naturalist Club in Knutsford, British Columbia, Canada (50.62°N, 120.33°W) from May to August 2011–2014. Every 1–3 d, we recorded the number

Figure 1. Hole opening nest box (left) and slot opening nest box (right).

of eggs laid ($n = 531$), number of nestlings ($n = 459$), and number of fledglings ($n = 341$) for each nest box ($n = 101$ boxes: 72 hole boxes, 29 slot boxes). Hole and slot entrance boxes were distributed across routes relatively evenly (Table 1); other than the clear difference in entrance hole construction, both slot and hole nest boxes were made of 0.5 inch plywood and did not vary systematically in their construction. Parents at these boxes were caught and each banded with a unique combination of an aluminum Canadian Wildlife Service band and 3 color bands.

Table 1. Number of hole and slot boxes occupied by Mountain Bluebirds on each monitoring route. Edith Lake, Jackson Rd, and Long Lake were used in primary analyses; the remaining boxes were only used for an expanded sample to examine the effect of box type on fledging success.

Route name	Hole boxes	Slot boxes
Campbell Range	19	2
Dewdrop	2	0
Edith Lake	6	8
Jackson Rd	15	5
Juniper	1	0
Lac du Bois	18	4
Long Lake	22	4
Pritchard East	20	0
Rosehill 1	15	8
Rosehill 2	23	0
Rosehill 3	25	0
Rosehill Ranch	9	1
Scott Rd	2	9
South Thompson	62	0

Parental provisioning rates were quantified during the early nestling stage (3–5 d after hatching) and the late nestling stage, (14–16 d after hatching), as described in Morrison et al. (2014) and Evans et al. (2015). Early and late provisioning rates were strongly correlated ($n = 72$, $r = 0.37$, $P = 0.001$). Sample size was smaller in the late nestling stage because of mortality occurring between these 2 stages, so only early nestling stage provisioning was included in our analysis. Parents at each nest were video recorded for 2 h periods with a Sony Handycam DCR-SX45 (Sony, Toyko, Japan), a GoPro HD Hero2, or a GoPro HD Hero3+ (GoPro, San Mateo, CA). Cameras were stationed on a fencepost ~5–10 m away from the nest. Video recordings began on average at 09:15 (SD 80 min), and provisioning rates were quantified as the number of trips to the nest per hour per chick for both parents, after removing the first 10 min of recording to allow time for the birds to acclimatize to the presence of the camera. Provisioning rates ranged from 0.4 to 18.8 trips/h/chick (mean: 6.01[SD 3.22] trips/h/chick). Our methods followed Balenger et al. (2007) and are consistent with previous work quantifying parental provisioning rates (e.g., Moreno et al. 1997, Smiseth et al. 2001, Germain et al. 2010, Osmond et al. 2013).

Weather data

We obtained local weather information by accessing online Environment Canada weather station archives for the Kamloops Pratt Road station, located at 50.60°N, 120.20°W, ~10 km from our study site. We calculated the mean temperature and total rainfall during the nestling period for each active nest along each route for each year from 2011 through 2014. The nestling period was defined as the time from the day eggs hatched to the day offspring fledged for each nest. Rainfall ranged from 0 to 68.6 mm during the nesting period (mean: 30.41 [SD 16.64] mm) while the average temperature ranged from 15.5 to 24.4 °C (mean: 17.90 [SD 2.31] °C).

Statistical analyses

To determine whether reproductive success differed between box types, we constructed linear mixed models with number of eggs laid, hatching success (number of nestlings/number of eggs laid), and fledging success (number of fledglings/number of eggs laid) as response variables and nest box type (slot or hole) as a main effect. To account for multiple years of data and individuals present in multiple years, we used year and female band number as random effects to avoid issues of pseudoreplication. Because other microclimatic factors and individual factors may influence reproductive success, we also included the following fixed effects: male age, female age, aspect of nest box opening, distance to the nearest tree, distance to nearest Mountain Bluebird, distance to nearest Tree Swallow nest, elevation, and percent tree cover within 100 m. We then used a backward stepwise procedure to eliminate nonsignificant effects and arrive at a final best fit model using a conservative alpha value of 0.10 to ensure we captured potentially important habitat effects. We also conducted a simple nominal logistic regression to ask whether male or female size (wing chord, tarsus length, tail length) predicted nest box type.

We used piecewise structural equation modelling (SEM) to investigate the correlations among fledging success, weather conditions, and parental provisioning rates. We created a path analysis diagram to visualize the decomposition of these relationships with each piecewise model in the structural equation. We constructed 16 models that related fledging success (as defined above) to the direct effects of mean nestling period temperature, total nestling period rainfall, and provisioning rate, and to the combined effects of temperature and rainfall, temperature and provisioning rate, rainfall and parental care, and temperature, rainfall and provisioning rate. Because we found no correlation between provisioning rate and time of observation, we did not include time of observation in our models. We included box number as a random effect in all models. Models were run separately for hole and slot nest boxes (discussed later). The fit of each model in the SEM was determined using D-separation tests, and models were compared using Akaike's information criterion adjusted for small sample size (AICc), estimated from D-separation tests (Shipley 2013).

Results

Comparing the success of Mountain Bluebirds in boxes with the 2 different types of entrances (n = 72 hole, 29 slot) as well as age and several microclimate characteristics, we found that entrance type was the greatest predictor of reproductive success (Table 2). Birds nesting in hole boxes produced significantly more eggs ($F_{1,95.44} = 4.98$, $P = 0.03$) and experienced significantly greater fledging success ($F_{1,93.66} = 4.46$, $P = 0.04$; Fig. 2) than did those nesting in slot boxes. Percent tree cover within 100 m was also marginally positively associated with fledging success ($F_{1,89.56} = 3.71$, $P = 0.06$). Neither box type nor any other microclimate characteristic was associated with hatching success. No differences in body size of either males or females was noted between box types (all $P > 0.17$). Because of the observed difference in reproductive success between hole and slot boxes, we utilized an expanded dataset to examine fledging success across 147 (2013; $n = 122$ hole, 25 slot) and 134 (2014; 117 hole, 17 slot) active

Table 2. Best fit linear mixed models explaining variation in number of eggs laid, hatching success (number of nestlings/number of eggs), and fledging success (number of fledglings/number of eggs) of Mountain Bluebirds, using nest box type, aspect of nest box opening, distance to the nearest tree, distance to nearest neighbour, elevation, and percent tree cover within 100 m as main effects, and box number and year as random effects.

Factor	Estimate	SE	*F*	df	*p*
Number of eggs					
Box type	5.17	0.09	4.72	52.8	0.03
Hatching success					
—	—	—	—	—	—
Fledging success (number fledged/clutch size)					
Box type	0.100	0.040	2.23	37.31	0.03
Percent tree cover	0.008	0.004	2.21	51.65	0.03

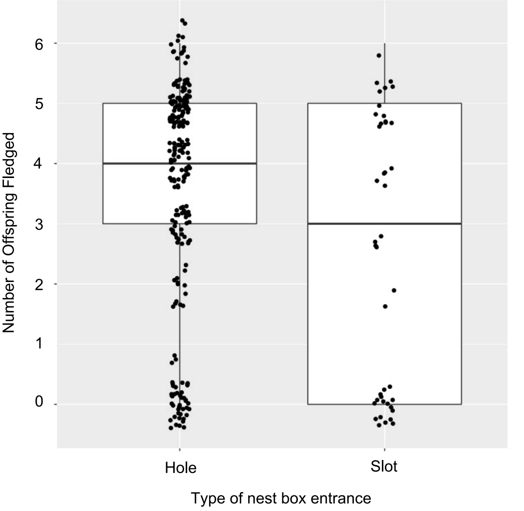

Figure 2. Box plot illustrating the number of offspring fledged; nest boxes with slot entrances had significantly lower fledging success. Box illustrates the median and interquantile range (IQR), while whiskers are 1.5 × IQR.

Mountain Bluebird boxes monitored by the Kamloops Naturalists Club. Similar to our results, a linear mixed model using this larger sample revealed a strong effect of box type on fledging success ($F_{1,157.4} = 8.15$, $P = 0.005$). Complete nestling mortality was more common in slot boxes (logistic regression: $\chi^2 = 9.07$, $P = 0.003$).

Because of the significant differences we observed in reproductive success between box types, we ran separate path analyses for hole and slot boxes. For hole boxes, both weather and provisioning rate exerted strong effects on fledging success. Provisioning rate was the best predictor of, and explained the most variance in, fledging success based on a comparison of model fit (P) and AICc (Table 3). When considering SEM linear coefficients, the effect of parental care was positive and that of temperature was negative (temperature: $\beta = -0.21$, $P = 0.04$; parental care: $\beta = 0.31$, $P = 0.01$; Fig. 2, Table 4), indicating that higher levels of provisioning, and to a lesser extent lower temperatures, were associated with higher fledging success. For slot boxes, the model that explained the most variance in fledging success included provisioning rate (Table 3), but when considering SEM linear coefficients, the effect of provisioning rate was nonsignificant ($\beta = 0.14$, $P = 0.22$; Fig. 3, Table 4).

Discussion

Many studies have assessed the influence of local weather and provisioning rates on reproductive success separately (e.g., Grant et al. 2000, Hoset et al. 2004). Few, however, have simultaneously evaluated the relative influence of these 2 factors (e.g., Öberg et al. 2015). Here, we examined the effects of parental provisioning and the direct and indirect effects of weather on the reproductive success of a population of Mountain Bluebirds breeding in a semiarid grassland of interior British Columbia. We found that the direct effects of provisioning rate and temperature were the best predictors of Mountain Bluebird fledging success. Although fledging success of Mountain Bluebirds was associated with provisioning rates and breeding season temperature, this association was dependent on nest box opening type, a finding that has important implications for naturalist clubs and citizen scientists constructing nest boxes for bluebirds. Most notably, reproductive success was higher in nest boxes with hole-shaped entrances compared to those with slot-shaped entrances (Fig. 2), after accounting for other potential microclimate differences among boxes.

Parental provisioning rates were strongly correlated with fledging success (number fledged/number eggs) in hole boxes (Fig. 3, Table 4). This result is consistent with other work demonstrating the importance of parental care in influencing the success of nestlings (e.g., Wright et al. 1998,

Table 3. Candidate path models created using piecewise SEM path analysis to evaluate the effect of temperature (temp), rainfall, and provisioning rates on the fledging success of Mountain Bluebirds.

Model	Fit (P)	K	AICc	Δ AIC
Hole boxes				
Parental care	0.11	3	13.88	0
Temp	0.05	3	15.71	1.83
Temp + rainfall	0.01	4	17.29	3.41
Null	0.01	2	19.46	5.58
Rainfall	0.005	3	21.36	7.48
Parental care + rainfall	0.15	7	25.11	11.23
Parental care + temp + rainfall	0.11	8	25.82	11.94
Parental care + temp	0.1	7	26.46	12.58
Slot boxes				
Parental care	0.80	3	8.6	0
Null	0.50	2	9.822	1.22
Temp	0.49	3	10.37	1.77
Temp + rainfall	0.33	4	11.9	3.3
Rainfall	0.25	3	12.36	3.76
Parental care + temp	0.93	7	21.22	12.62
Parental care + temp + rainfall	0.80	8	24.84	16.24
Parental care + rainfall	0.47	7	24.96	16.36

Table 4. Linear coefficients from the structural equation model decomposing independent weather and parental provisioning effects on the fledging success of Mountain Bluebirds.

Hole boxes			Slot boxes		
Estimate	Standard error	*p*	Estimate	Standard error	*p*
−0.21	**0.1**	**0.04**	0.26	0.28	0.36
0.005	0.015	0.77	0.006	0.029	0.84
0.31	**0.12**	**0.01**	0.17	0.14	0.22

Rauter et al. 2000). We did not directly assess the mechanism driving increased fledging success, but previous work has linked increased provisioning to nestling growth rates (Klug and Bonsall 2014) and condition (Soma et al. 2006, Wilkin et al. 2009). While we were not able to quantify the amount or quality of food delivered per visit, our results nonetheless indicate provisioning rate is an important driver of reproductive success in Mountain Bluebirds, which may potentially buffer against the effects of adverse weather conditions.

While provisioning rate was the most important determinant of reproductive success, temperature also exerted an effect on Mountain Bluebird reproduction, although this effect was dependent on the type of nest box opening. For birds nesting in boxes with hole-shaped entrances, higher temperatures were associated with reduced fledging success. This contrasts with findings in other species that demonstrate improved hatching success (Martin 1987) and fledging success (Reid et al. 2000, Ardia et al. 2010) when weather is warmer. One possibility for our different result is that the effect of lower temperatures is indirect and actually related to earlier nesting, which is often associated with larger clutch sizes (Klomp 1970, Crick et al. 1993, Brown and Brown 1999) and increased reproductive success (Lozano et al. 1995, Reudink et al. 2009). If that were the case, however, we might have expected birds nesting in

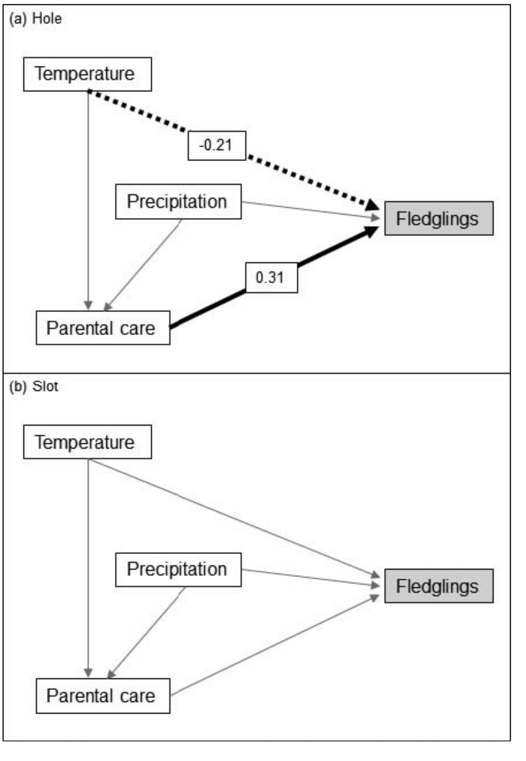

Figure 3. Path analysis of mean nestling period temperature, total nestling period rainfall, and total parental provisioning on fledging success of Mountain Bluebirds (proportion of eggs that fledged) for hole- and slot-opening type nest boxes. The thickness of the arrows represents the magnitude of the effect (β; shown in parentheses) as well as the significance. A solid black arrow indicates a significant positive effect; a dotted black arrow represents a significant negative effect.

hole boxes to lay their clutches earlier, but no difference was noted in first egg dates between birds nestling in hole and slot boxes at our study site (MWR unpubl. data).

Birds nesting in boxes with hole-shaped entrances had significantly higher productivity; Mountain Bluebirds nesting in these boxes laid more eggs and experienced greater fledging success. Despite Mountain Bluebirds generally preferring open grassy areas, we also detected a weak positive effect of percent tree cover on fledging success, possibly due to greater foraging opportunities with more tree cover. Our study site is largely composed of grasslands, however, so this possibility would require further study. Because the size of a nest box entrance can determine how much protection it offers to its occupants (Lambrechts et al. 2010), boxes with hole-type openings may provide better shelter from exposure (e.g., to wind and rain entering the nest especially during cold spells) and predation. We found greater total nest failure in boxes with slot-type entrances, which reinforces the idea that a high degree of exposure likely accounted for a high level of mortality. Interestingly, we found no influence of weather on fledging success for birds nesting in slot boxes, in contrast to the situation for hole boxes. Perhaps hole boxes, although providing better protection in most weather conditions, become overheated in hot weather, thus contributing to greater nestling mortality in these situations, although we note this has not been observed in our population. More research into the differences in insulative properties between box types would be needed to test such a hypothesis. Another possible contributing factor to the differences in productivity between hole boxes and slot boxes is that differences in individual quality existed among individuals nesting in each type of box. Although we detected no difference in the ages or body size of birds nesting in each type of box, birds selecting hole and slot boxes possibly differed in some other measure of quality.

In conclusion, we demonstrate that nest box type, provisioning, and temperature all have important effects on reproduction in Mountain Bluebirds. Birds nesting in hole boxes experienced greater reproductive success, and the influence of weather on fledging success was more apparent for these birds, perhaps because of differences in insulative properties between box types. Our results reinforce the need for more research into the influences of nest box characteristics on reproductive success (Lambrechts et al. 2010), especially for species such as the Mountain Bluebird, whose populations are heavily dependent on nest box programmes (Power and Lombardo 1996). Furthermore, we recommend the use of nest boxes with hole-shaped entrances over those with slot-shaped entrances for managers and conservationists interested in aiding populations of Mountain Bluebirds, although we caution that more research is needed to determine the mechanisms underlying the differences in reproductive success between box types.

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