

**VARIATION IN NEST DEFENCE AND INCUBATION BEHAVIOUR IN MOUNTAIN
BLUEBIRDS (*SIALIA CURRUROIDES*) IN RELATION TO NEST PREDATION**

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By

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ABSTRACT

The predation of nestlings represents a high cost to birds that during the incubation and nestling stage of their development. Consequently, predation likely shapes various aspects of parental behaviour in birds that exhibit parental care.

Within any given species, parent birds defend their nests with different levels of intensity. Previous studies have examined several hypotheses for this variation by examining factors such as morphological characteristics of parents and characteristics of the brood, but few have controlled for multiple factors simultaneously. Here I examined a broad range of factors that may influence the nest defence behaviour of Mountain Bluebirds (*Sialia currucoides*), including morphology of adults (sex, age, plumage colour, body size, and body condition) and characteristics of broods (size, hatch date, and stage of offspring development). An essential aspect of parental behaviour in birds is the incubation of eggs. Maintaining the eggs at a suitable temperature for embryonic development requires time and energy and this must be traded-off with requirements for foraging and self-maintenance. I examined how exposure to a nest predator altered the incubation rhythms of female Mountain Bluebirds and for how long such variation lasted.

I studied the intensity of nest defence behaviour and incubation rhythms breeding pairs of Mountain Bluebirds in response to a model nest predator in the central interior of British Columbia. Parental aggression was triggered using a taxidermy mount of an american red squirrel (*Tamiasciurus hudsonicus*), which is the main predator of eggs and nestlings in the study area. My research had two main objectives: 1) to test whether one sex generally invests more effort in nest defence and whether an individual's investment is related to characteristics of the

brood and/or the parents.), and; 2) to examine whether the incubation rhythms of females change in response to predation risk and how long these changes may last.

I found no relationship between nest defence and the morphological characteristics of adults that I quantified, but the intensity of nest defence was positively correlated with the stage of offspring development, clutch size, and hatch date consistent with parental investment theory. Males also defended nests more strongly than females, consistent with the premise of the renesting hypothesis that males have fewer future opportunities to breed and, therefore, are more invested in the current brood. My results provide strong support for parental investment theory and renesting as the primary drivers of nest defence intensity in breeding birds.

I found that following exposure to a model nest predator, incubating females reduced the number of times they left the nest, consistent with the hypothesis that they were minimizing the risk of attracting the attention of a nest predator. At the same time, they increased the length of recesses to potentially forage enough to maintain an energy balance. These changes in incubation rhythms were relatively short-lived with the female resuming normal incubation behaviour two days after exposure to a model nest predator. The constancy of incubation (% of time on nest) did not significantly change before or after the predator trial, suggesting that female Mountain Bluebirds place a high priority on regulating the temperature of the eggs even during the threat of nest predation. The incubation rhythms were not influenced by the age and body condition of the female. The external ambient temperature did not affect any aspect of incubation behaviour before exposure to the model predator. However, there was a negative correlation between constancy and ambient temperature after the model predator was presented.

My study is among the first to test the parental response regarding nest defence and incubation rhythms to the risk of predation while controlling for multiple factors at the same

time. The results of this study suggest that these aspects of parental behaviour were driven primarily by the sex of parent and reproductive value of the brood rather than the morphological characteristics of the parents. My results also suggest that incubating females minimized their activity around the nest following exposure to a model nest predator without significantly altering constancy on the nest.

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CHAPTER 1: GENERAL INTRODUCTION

1.1 Parental Response to Nest Predation

Most passerine birds exhibit biparental care but the absolute amount of care that each sex invests and/or the stage of breeding at which each invests may differ (Clutton-Brock 1991). For example, female birds are often expected to invest more effort in the current brood than the male (Barash 1976, Stearns 1989) because they can be certain the offspring in the nest are theirs, whereas males are less certain the offspring they are guarding was fathered by them.

Parental investment in birds has been studied mainly during the nestling period, in the context of food provisioning. However, parental investment includes a variety of behaviours at different stages of breeding that maximise the fitness and survival of offspring such as nest building and maintenance, incubation, and protection from predators (Clutton-Brock 1991, Klvanova et al. 2011). In many birds, loss of the eggs or nestlings to predators is a catastrophic event that can significantly reduce reproductive success (Ricklefs 1969). Although parents are probably highly motivated to defend their offspring, nest defence is one of the most costly activities for a parent because it may risk its own survival while preventing a predator from killing the young (Montgomerie and Weatherhead 1988, Hogstad 2005).

In many socially monogamous bird species, both parents contribute to nest defence (Skutch 1955), but the exact roles and the amount of effort made in defending their progeny often differs between the sexes for reasons that are not fully understood (Lima 1993, Wesolowski 1994). In some species, either males (Nado et al. 2018) or females (Weatherhead 1979) seem more inclined to defend the nest than the other sex. In still other cases, within a species, sex-specific levels of defence can vary with the type of predator or with the stage of

breeding. For example, Hogstad (2005) found that female Fieldfares (*Turdus pilaris*) defended more than males when presented with nest predators that were less threatening to adults themselves (a human coming close to the nest, or a model crow placed close to the nest) but less than the male when faced with a predator that was more dangerous to the adult (a model Sparrow hawk (*Accipter nisus*)).

Other key factors in nest defence appear to be the perceived quality of the brood itself with parents likely to defend older offspring due to their increased chances of survival or the limited possibility of the parents renesting (Andersson et al. 1980, Strnadova et al. 2018). In addition, larger clutch or broods may be defended more as they are perceived to be of higher value to their parents.

An essential aspect of parental behaviour in birds is the incubation of eggs. Maintaining the eggs at a suitable temperature for embryonic development requires time and energy (Mallory and Weatherhead 1993, Williams 1996) and this must be traded-off with requirements for foraging and self-maintenance (Wiebe and Martin 1998). With predation shown to be one of the primary causes of nest failure in most avian species (Ricklefs 1969, Martin 1993), there is likely selection on incubation patterns to minimize detection of the nest by predators.

Research on Song Sparrows (*Melospiza melodia*) suggests that even the perception of predation risk alone will reduce the number of offspring produced in the same year by as much as 40% (Zanette et al. 2011). This would suggest that in passerine species, incubating parents are under extreme pressure to avoid predation while at the same time maintaining optimal incubation rhythms (limited fluctuations in egg temperature). This may also indicate that parents may feel threatened after the immediate threat has passed because of they may perceive that the predator

is still present. Therefore, there could be trade-off between returning to normal incubation rhythms to maximize optimal incubation temperature and limiting the exposure of eggs and offspring to predation.

As first proposed by Skutch (1949), visits by bird parents to the nest will draw the attention of predators to the location of the offspring. Several studies have experimentally increased the perceived predation risk and observed that female birds counter this risk by reducing the frequency of incubation recesses (Basso and Richner 2015), increasing incubation constancy (% of time on nest), or decreasing conspicuous incubation behaviour (Smith et al. 2012) such as spending time around the nest. While the risk of predation does seem to influence incubation rhythms over the course of the incubation stage of reproduction, there is still limited information on how incubation rhythms are affected immediately following an encounter with a model nest predator and whether the lingering effects of a perceived risk of nest predation may influence a return to normal incubation behaviour.

1.2 Study Species and Field Site

The Mountain Bluebird (*Sialia currucoides*) is an insectivorous cavity-nesting thrush weighing about 30 g that nests in grasslands, clear-cuts, and burns throughout northwestern North America (Johnson and Dawson 2020). Males are slightly larger than females and the sex of parents is easy to distinguish in the field according to clear sexual dimorphism in plumage colour (Johnson and Dawson 2020). The study was conducted in central British Columbia, Canada, from April to June 2019 near Bridge Lake (51.48°N, 120.7°W; 1140 m above sea level (a.s.l.)), 100 Mile House (51.64°N, 121.3°W; 970 m a.s.l.), and Riske Creek (51°58' N, 122° 31' W, 986 m a.s.l.) (Figure 1.1). More than 300 plywood nest boxes (16 X 16 X 30 cm with a 4 cm

diameter entrance hole) were placed on retained trees in logging cuts and on fence posts in grazed grasslands (see Stalwick and Wiebe 2019a).

Mountain Bluebirds arrive at the study areas each year around mid-April following migration. Males establish a territory around a potential nesting cavity and displaying it to the female (Power 1966). Females on average lay clutches of 5 to 6 eggs (Stalwick and Wiebe 2019b) and incubate, but both parents provision the offspring with a variety of invertebrate prey (Power 1980, Herlugson 1982, Stalwick and Wiebe 2019b), and the nestlings fledge after 15-22 days (Johnson and Dawson 2020). From 5% to 34% annually of females in the population attempt a second brood after fledging the first, and nestlings fledge from broods initiated as late as 8 July (K.L. Wiebe, unpublished data). All broods in the current study, however, were first broods initiated on or before 28 May.

The conspicuous structure of nest boxes makes their occupants potentially vulnerable to nest predators (Johnson and Dawson 2020). The nests of mountain bluebirds are preyed upon by a range of predators such as black bears (*Ursus americanus*) (Johnson and Dawson 2020), short-tailed weasels (*Mustela erminea*) (Chalmers 1981), american red squirrels (*Tamiasciurus hudsonicus*) (Stalwick and Wiebe 2019a), and Black-billed Magpies (*Pica hudsonia*) (Pearman 1991). In my study area, nest predation is primarily caused by american red squirrels (Stalwick and Wiebe 2019a). Robles and Martin (2013) found that nest predation was attributed to 57% of known nest failures in natural cavities in their study site close to mine in central British Columbia.

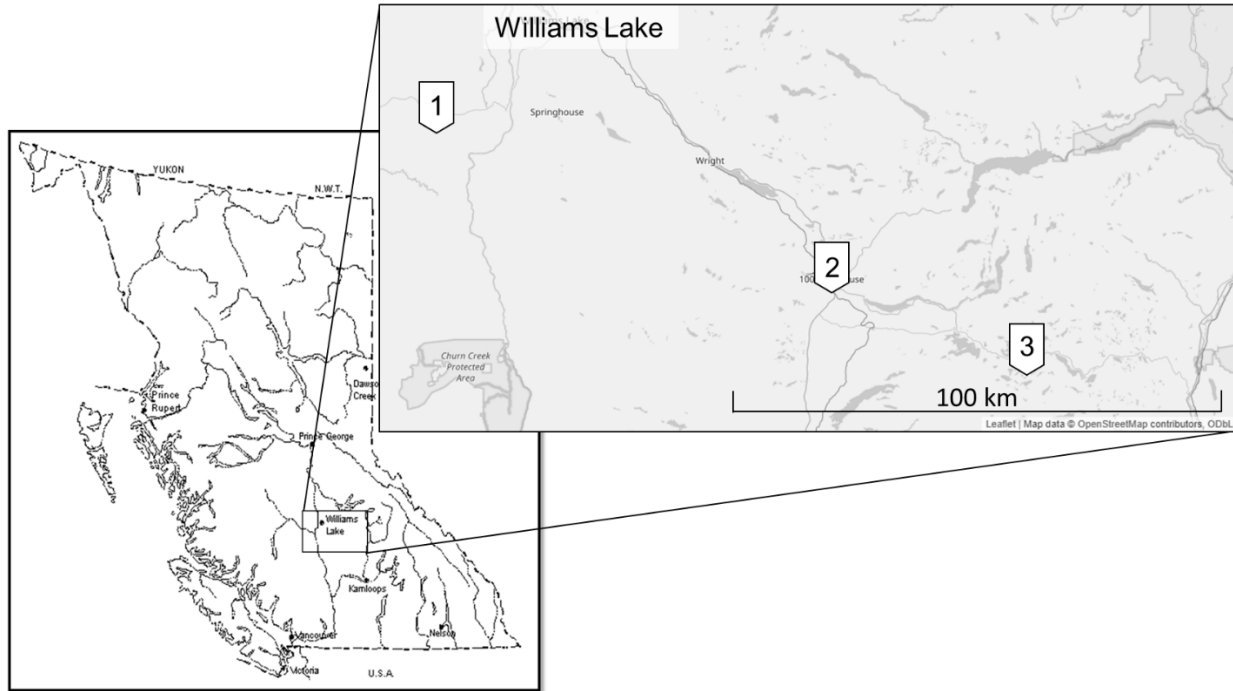


Figure 1.1. A map of the three study sites in central British Columbia, Canada. The box on the right is an enlarged map of the area within the box in the map of British Columbia on the left. The 1 indicates Riske Creek, the 2 is 100 Mile House, and the 3 is Bridge Lake.

1.3 General Field Methods

Nest boxes were monitored approximately every 3 days to determine clutch size, hatch date, and the number of nestlings. While provisioning their young (during nestling ages 3-13 Days after hatching), parents were trapped in the nestbox using a swing door trap. Each individual was banded with a unique combination of a single numbered aluminum band and three colour bands for future identification, and I determine age as either a yearling (SY) or adult (>1 year, ASY) based on the molt of the secondary coverts (Pyle 1997). A secondary feather (S2) was clipped for later colour analysis in the laboratory. Captured parents (male $n = 41$, female $n = 40$) were weighed and the length of the combined head and bill, culmen, tarsus, central rectrix, 10th primary flight feather, and flattened wing chord were measured.

Temperature in the nest bowls ($n = 42$) was recorded using iButtons (Maxim Integrated; <https://www.maximintegrated.com/en.html>) to calculate the timing and length of incubation recesses. iButtons have been used to monitor incubation fluctuations in a wide range of birds species (Smith et al. 2015, Walters et al. 2016) including Mountain Bluebirds (Johnson et al. 2013a). All the trapping and banding was conducted under Animal Care permit 20160018 from the University of Saskatchewan.

1.4 Predator trial

Gibson and Moehrensclager (2008) investigated the aggression of Mountain Bluebirds by using a taxidermic mount of a bobcat (*Lynx rufus*), but this is not a typical predator of nestlings, so I presented parent bluebirds with a model of an american red squirrel, the main predator of eggs and nestlings on the study area (Stalwick and Wiebe 2019a). When the adults are not in the nest box, a squirrel poses a risk to the nest contents but not to parents.

The predator model was placed on the roof of the nest box and presented to 54 bluebird pairs during the incubation stage, 4-6 days after the last egg had been laid, and again during the nestling stage when offspring were 11 days old. Before a trial, a small camouflage blind was placed about 40 m from the nest box to conceal me, and a video camcorder (Panasonic HDC-SD80) was placed on a tripod approximately 5 m from the nest box to record the aggressive behaviours of parents towards the model at close range. When at least one parent appeared within 50 m of the box, a fishing line attached to a small cloth covering the squirrel was pulled to reveal it. Parental responses were recorded for 5 minutes to record a sufficient number of behaviours while minimizing habituation to the model. Afterwards, the squirrel model was removed.

1.5 Objectives

The main objective of my thesis was to examine how the parental behaviour of Mountain Bluebirds was affected by the immediate threat of a nest predator. Specifically, I investigated how individual variation in active defence behaviour and incubation rhythms were related to several morphological traits of the parent, features of the brood, and abiotic conditions like ambient temperature. The specific questions and hypotheses I tested in each chapter are outlined below:

In Chapter 2, I examined how the intensity of nest defence was influenced by multiple morphological characteristics of the parents and the characteristics of the brood. Various hypotheses exist to explain the intensity of nest defence based on sex, morphology, and the reproductive potential of the offspring.

The larger body size of one sex (Svagej et al. 2012), usually males, and depletion of energy reserves during egg formation and incubation by females (Williams 1996), might suggest that the intensity of nest defence will be higher in males. Alternatively, the paternity hypothesis

(Winkler 1987, Westneat 1988) suggests males will defend less intensely than females because they are less certain of their genetic relatedness to the offspring.

Larger individuals with abundant nutrient reserves are also predicted to defend more because defence will be relatively less costly for them (Hogstad 2005, Unzeta et al. 2020). A higher intensity of nest defence is expected in older individuals that are more experienced and less likely to reproduce in the future (Pearson et al. 2005). Recently, plumage colour has been suggested as an honest visual cue of parental investment, including the intensity of nest defence (Segura and Mahler 2019).

The squirrel model was presented to a bluebird pair twice: once during the incubation stage and once during the nestling stage. Parental investment theory suggests that parents should defend high-value offspring with a greater intensity than those of lower value (Trivers 1972). Nests that contain older offspring and larger clutches or broods may be perceived to be more valuable to their parents because they are more likely to survive and breed themselves and may therefore be defended more aggressively. The lower probability of renesting later in the breeding season may also make older offspring more valuable to their parents (Andersson et al. 1980, Strnadova et al. 2018). While previous studies have examined variation in defense in relation to these factors, few have controlled for multiple factors simultaneously.

In Chapter 3, I examined how incubation rhythms may change in response to the direct exposure of a model nest predator, and how long any changes in rhythms persisted afterward. Several hypotheses attempt to explain potential changes in incubation rhythms associated with a perceived encounter with a nest predator.

To test Skutch's (1949) hypothesis that the risk of predation will reduce parental visits to the nest immediately following exposure to a nest predator, I placed iButtons in the nest both before and immediately after the predator trial at the incubation stage to test for changes in incubation behaviour. The threat posed by a model nest predator could result in the female limiting recess rates after exposure to this perceived danger (Basso and Richner 2015). This would lead to a higher constancy and longer recesses to maintain her energy levels to continue incubating (Skutch 1962). Alternatively, survival may take precedence for the female over the safety of the eggs. This would make her more cautious of further intrusions that may threaten her safety. Therefore, the recess rate may increase as she tries to limit her time in the nest box.

I also examined whether any changes in incubation rhythms were related to a range of morphological and behavioural traits of females. During incubation, incubating parents face a trade-off between maintaining their body condition and their incubation requirements (Mitchell et al. 2012). In general, birds in better body condition are more attentive to their nests (Gorman and Nager 2003), likely due to requiring less time to replenish their body reserves. Incubation rhythms may therefore be more stable in individual in better body condition.

Age has may also influence potential incubation fluctuations caused by predation. Older and more experienced females spend more time incubating the eggs (Ardia and Clotfelter 2007) possibly due to being generally more efficient at finding food (Wunderle 1991) and choosing better quality nesting sites (Amininasab et al. 2016). The active aggression towards a nest predator may successfully deter future attacks (Blancher and Robertson 1982, Svagelj et al. 2012). Therefore, more aggressive individuals may feel more confident that the threat from the model predator has abated will not alter their incubation behaviour as much as less aggressive females.

In addition, I placed iButtons outside the nest box to test for ambient temperature during this time. Lower ambient temperature outside the nest places pressure on the female to increase incubation constancy (Tinbergen and Williams 2002, Cresswell et al. 2004) to prevent temperature fluctuations that could hinder development of the eggs (Webb 1987).

1.6 Thesis Format

This thesis has been structured in manuscript format for publication. Consequently, there may be some repetition of information throughout the text. Chapter 2 has been published in full in *Canadian Journal of Zoology* under joint authorship with Doug Chivers and Karen Wiebe. Chapter 3 is currently being revised and reformatted for publication.

CHAPTER 2: NEST DEFENCE BY MOUNTAIN BLUEBIRDS IS RELATED TO THEIR SEX AND BROOD CHARACTERISTICS BUT NOT MORPHOLOGICAL ATTRIBUTES

2.1 Introduction

Nest predation is among the leading causes of reproductive failure for most passerine species (Ricklefs 1969), sometimes causing the loss of half of the nests in a population (Martin 1993, Jara et al. 2020). To counter predation risk, parents use a variety of active and passive defence mechanisms, such as building nests away from areas where predators are known to be abundant (Vernouillet et al. 2020), camouflaging nests and eggs (Troscianko et al. 2016, Stevens et al. 2017), and actively attacking predators to defend their nests (Redmond et al. 2009). Attacking a predator is one of the most expensive activities for a parent in terms of energy expenditure and the risk to its survival (Regelmann and Curio 1986, Montgomerie and Weatherhead 1988), yet it often receives less attention than provisioning behaviour. There are many factors that potentially affect the intensity of nest defence, including the type of predator, past experience, morphological attributes of the parents, and characteristics of the brood (reviews in Montgomerie and Weatherhead 1988, Clutton-Brock 1991). To date, most studies have addressed only one or two factors at a time, but here, I simultaneously assessed multiple factors, testing for an association between the intensity of nest defence and parental size, condition, colour, and age, as well as brood attributes (size and age/stage) and time remaining in the breeding season.

Several predictions about the intensity of nest defence are based on life-history and parental investment theories. Defence should increase with parental age, as the number of future reproductive opportunities declines (Pearson et al. 2005) and parents with abundant nutrient

reserves should be more willing to defend intensely since they likely have more energy available than parents in poor condition (Wallin 1987, Hogstad 2005). Parents should also increase the defence of broods with greater reproductive value (Trivers 1972), typically those with older offspring either because those offspring have a greater chance of reaching maturity or because there is a lower probability of renesting as the season progresses (Andersson et al. 1980, Strnadova et al. 2018). However, offspring hatched late in the season may not be well-defended if they are of poor quality (e.g., Brown and Brown 1999). In addition, parents are predicted to defend larger clutches or broods more intensely than small ones (Redondo 1989, Svagelj et al. 2012), as these generally produce more fledglings and will be of higher value to parents.

With respect to morphological attributes of parents, larger individuals may defend more intensely because a large structural size is generally thought to reduce the considerable risk of injury associated with confronting a nest predator (Weidinger 2002, Unzeta et al. 2020, Andersson and Wiklund 1987). More recently, plumage colour, a potential indicator of nutritional status and quality in birds, has garnered interest as an honest visual cue of parental investment (Segura and Mahler 2019). Although colour, unlike body size, would not influence the effectiveness of nest defence directly, ornamentation may be correlated with an attribute such as age/experience or body condition which does (Morrison et al. 2014). In Eastern Bluebirds (*Sialia sialis*), the greater reproductive success of more colourful parents was attributed to their higher provisioning rates (Siefferman and Hill 2003, Siefferman and Hill 2005) consistent with the “good parent” hypothesis for ornamentation, but nest defence levels were not examined. Therefore, I was interested in testing whether bright plumage colour was positively correlated with the intensity of nest defence, an unexamined aspect of parental care, in Mountain Bluebirds (*Sialia currucoides*).

With respect to sex-specific defence, two hypotheses predict that males should defend more intensely than females and one hypothesis predicts the opposite. In size dimorphic species, the larger sex, typically the male, should exhibit higher levels of nest defence (Svigelj et al. 2012). Second, if females deplete their energy reserves in early breeding stages when forming and incubating eggs (e.g., Williams 1996, Fontaine and Martin 2006), they may be less willing and/or able than males to expend energy on defence if it jeopardizes their opportunities for future reproduction. In contrast, the paternity hypothesis (Winkler 1987, Westneat 1988) suggests males will defend less intensely than females if they are uncertain of their genetic relatedness to the brood.

In addition to examining features of the parents and features of the brood directly, I was curious how the relative contributions by males and females may change over time as breeding progresses from the incubation to nestling stages of reproduction, which has been rarely addressed by other studies (Hogstad 2005). I measured the intensity of nest defence of parent Mountain Bluebirds using predator presentation trials of a common nest predator, the american red squirrel (*Tamiasciurus hudsonicus*), predicting that nest defence would be positively correlated with parental age, size, and body condition and that the intensity of nest defence would be higher for broods perceived to be more valuable (older, hatching later in the season and with more offspring).

2.2 Materials and Methods

2.2.1 Study Site and Species

The Mountain Bluebird is an insectivorous cavity-nesting thrush that breeds throughout northwestern North America in grasslands, clear-cuts, and burns (Johnson and Dawson 2020). Males are slightly larger than females and the sex of parents is easy to distinguish in the field

according to clear sexual dimorphism in plumage colour (Johnson and Dawson 2020). I conducted the study in central British Columbia, Canada, from April to June 2019 near Bridge Lake (51.48°N, 120.7°W; 1140 m above sea level (a.s.l.)) and 100 Mile House (51.64°N, 121.3°W; 970 m a.s.l.). More than 300 plywood nest boxes were placed on retained trees in logging cuts and on fence posts in grazed grasslands (see Stalwick and Wiebe 2019a). Each year, Mountain Bluebirds arrive at the study areas around mid-March following migration. Males establish a territory around a potential nesting cavity and displaying it to the female (Power 1966). Females lay clutches of five to six eggs, on average, (Stalwick and Wiebe 2019b) and incubate, but both parents provision the offspring with a variety of invertebrate prey (Power 1980, Herlugson 1982, Stalwick and Wiebe 2019b), and the nestlings fledge after 15–22 days (Johnson and Dawson 2020). From 5% to 34% annually of females in this population attempt a second brood after fledging the first, and nestlings fledge from broods initiated as late as 8 July (K.L. Wiebe, unpublished data). All broods in the current study, however, were first broods initiated on or before 28 May.

2.2.2 Field Methods

I monitored nest boxes approximately every 3 days to determine clutch size, hatch date, and the number of nestlings. While provisioning their young (during nestling ages 3–13 days), parents were trapped in the nestbox using a swingdoor trap. Each individual was banded with a unique combination of a single numbered aluminum band and three colour bands for future identification, and I determine age as either a yearling (SY) or adult (>1 year, ASY) based on the molt of the secondary coverts (Pyle 1997). A secondary feather (S2) was clipped for later colour analysis in the laboratory. Captured parents (male n = 41, female n = 40) were weighed and six measures of structural size were taken: lengths of the combined head and bill, culmen, tarsus,

central rectrix, 10th primary flight feather, and flattened wing chord. I entered these measures in a principal component analysis (PCA; one for each sex) and used the values from the first axis (first principal component, PC1) as a measure of overall body size (Rising and Somers 1989). I then calculated a body condition index using the residuals from a regression of body mass on PC1, as in Labocha and Hayes (2012) and Wiebe and Vitousek (2015). The trapping and banding was conducted under Animal Care permit 20160018 from the University of Saskatchewan.

2.2.3 Predator Experiment

Gibson and Moehrensclager (2008) investigated the aggression of Mountain Bluebirds by using a taxidermic mount of a bobcat (*Lynx rufus*), but this is not a typical predator of nestlings so I presented parent bluebirds with a model of an american red squirrel, the main predator of eggs and nestlings on my study area (Stalwick and Wiebe 2019a). When near the nest box (but not inside it), the squirrel poses a risk to the nest contents but not to parents. The predator model was placed on the roof of the nest box and presented to 54 bluebird pairs during the incubation stage, 4–6 days after the last egg had been laid, and again during the nestling stage when offspring were 11 days old.

Before a trial, a small camouflage blind was placed about 40 m from the nest box to conceal the observer during the predator presentation and a video camcorder (Panasonic HDC-SD80) was placed on a tripod approximately 5 m from the nest box to record the aggressive behaviours of parents towards the model at close range. When at least one parent appeared within sight of the box (i.e., within 50 m), a fishing line attached to a small cloth covering the squirrel was pulled to reveal it. Parental responses were recorded for 5 min. I chose a time of 5 min to record a sufficient number of behaviours while minimizing habituation to the model. Both

parents typically responded within a few seconds of each other, so there was no time bias limiting the number of hits or dives each sex could perform.

In cases where parental behaviour occurred outside the video camera frame, I recorded behaviours on a voice recorder, estimating the distance of the male and female from the model during the trial to within 1 m. Estimating distance of parents from the model was often facilitated by the even spacing of fence posts near the box or other perches near the box that could be measured directly. From the videos and from the observations, I extracted seven variables related to the intensity of defence: (1) distance of the parent from the model predator, measured every 15 s and then averaged over the trial (Average Distance), (2) the number of dives at the model (Dives), (3) the minimum distance between the parent and the model predator during a dive (Dive Distance), (4) the number of hits on the model (Hits), (5) the duration of time hovering near the model (Hover Time), (6) the total time during the trial spent on any active aggression (e.g., hovering, flying, and diving) towards the model (Aggressive Time), and (7) the time lag from when the model was revealed to when a parent first reacted to the model (Latency Time).

2.2.4 Extraction of Aggression and Colour Scores

To reduce the number of dependent variables for analysis while minimizing information loss, I used PCA to extract a single aggression score from the PC1 axis loadings, as done in other studies (Olendorf and Robinson 2000, Quesada and Senar 2007). Prior to the PCA, log transformations were done on Average Distance, Dives, Hits, and Latency Time to normalize distributions. With Average Distance, Dive Distance, and Latency Time measurements, the sign on the variable was also made negative so that larger values would indicate greater defence and match the directionality of other variables. The PC1 explained 67% of the variation in the data, with all seven aggression measures loading positively on this axis (Table 2.1). PCA was

conducted using SPSS version 26 (IBM Corp. 2019) and included both sexes because males and females displayed the same types of behaviour during trials.

2.2.5 Colour Analyses

Feather colour was analyzed with an Ocean Optics Flame Miniature Spectrometer with a DH-mini UV-VIS deuterium halogen light source and a white reflectance standard. The integration time was set to 325 ms, the average scans to 2, and the boxcar to 10 ms. Three readings were taken on the leading edge of the vane at 2.5 cm from the tip of each feather, following Stalwick and Wiebe (2019b). Four colour variables commonly used in studies of structural blue plumage were calculated: brightness, blue chroma, ultraviolet chroma, and hue (Montgomerie 2006, Berzins and Dawson 2016) using the R library “pavo” (Maia et al. 2013). Brightness represents the average amount of light reflected by the feather across the 300–700 nm spectrum (% reflected). The two chroma variables represent the proportion of light reflected by the feather in their respective ranges (blue range 400–512 nm, UV range 300–400 nm) relative to the 300–700 nm spectrum. Hue is the wavelength of maximum reflectance of the feather. Since hue and ultraviolet chroma were highly correlated for males ($r=0.90$), the latter variable was discarded for males and since hue and blue chroma were highly correlated among females ($r=0.82$), the latter variable was discarded for females.

I conducted another PCA to extract a single colour variable, performing separate analyses for the sexes because of the strong colour dimorphism. PC1 explained 53% of the variation in colour in males and 67% in females (Table 2.2). Thus, among males, high colour scores indicated hues near the shorter blue/UV wavelengths and high chroma saturation in the blue wavelengths. High colour scores for females indicated more reflective (“bright”) feathers but with less saturation in the short wavelengths (less blue and more green-shifted hues).

2.2.6 Statistical Analyses

In six trials during incubation and three during the nestling period, only the female parent appeared, so I tested whether the aggression level differed between females that reacted alone versus those that reacted alongside their mate. Since there was no difference either at the incubation ($t[5] = 0.42$, $p = 0.69$) or the nestling stages ($t[2] = -1.43$, $p = 0.28$), I included all females in subsequent models. Within each sex, I first tested whether any of the three morphological variables of body size, body condition, and colour differed between age classes with Welch's t tests. Where there was a difference between age classes (see Results section), subsequent models were run separately on each age class.

Since the aggression PCA score was a continuous and normally distributed dependent variable, I used general linear models (LMs) to test for the effects of the four parental morphological traits (body size, body condition, colour, and age). I needed to create separate models for each sex because of the clear sexual dimorphism in size and colour; separate models were also run for the egg stage and the nestling stage. Not all adults could be captured at all nests, making the sample size for these models smaller than the total number of trials conducted. I created LMs using the "lm" function in R version 3.6.1 (R Core Team 2019) and used type III sums of squares in the "Anova" function available from the "car" package (Fox and Weisberg 2019). Significance was set at $p < 0.05$.

To examine how the defence scores of males and females might change between the incubation and nestling breeding stages, I ran a repeated-measures linear mixed-effects model (LMM) with the aggression PCA as the dependent variable. The repeated measures design tests for changes within individuals across time (in this case, breeding stage) and controls for parental attributes like age and morphology. Since the same parents were tested at both breeding stages, I

entered parental ID as an independent random effect and tested for the fixed effect of sex and entered characteristics of the brood (brood size and hatch date) as covariates. This LMM was created using the “lmerTest” package in R version 3.6.1 (Kuznetsova et al. 2017) with significance set at $p < 0.05$. Degrees of freedom are rounded to the nearest integer because they are calculated estimates.

2.3 Results

2.3.1 Morphological Traits of Parents

Adult males had higher colour PC1 scores than yearlings and thus reflected more in the blue/UV spectrum ($t = 19.89$, $p < 0.001$). Adult males were larger than yearlings ($t = 4.95$, $p < 0.001$) but did not differ in body condition ($t = 1.12$, $p = 0.27$). For females, the age classes did not differ in any morphological measure: colour PC1 ($t = 1.77$, $p = 0.08$), body size ($t = 0.22$, $p = 0.82$), and body condition ($t = 0.50$, $p = 0.58$). Therefore, I ran separate LM models for each age class of males but pooled females of both age classes in models with morphological traits. No morphological characteristic of females or of males was associated with their level of nest defence at either the incubation or nestling stages (Table 2.3 and Table 2.4).

2.3.2 Characteristics of broods

Repeated measures analysis showed a significant interaction between sex and stage of breeding (Table 2.5). Graphing the interaction revealed that males defended more strongly than females at both breeding stages but the difference between sexes was greater during the nestling stage (Figure 2.1). Both sexes displayed higher mean aggression during the nestling stage than during the incubation stage (Table 2.5, Figure 2.1).

Brood size was a significant predictor of aggression in the model (Table 2.5) with parental defence increasing as the number of offspring increased from 5 to 6. (Figure 2.2). The mean clutch size among the pairs I studied was 5.8 ± 0.03 , $n = 55$, range 5–7; the mean brood size was 5.2 ± 0.05 , $n = 54$, range 2-6. Although parents with small broods (≤ 4) did not clearly defend with the lowest intensity, sample sizes of such broods were small and error bars overlapped with the others. Finally, nest defence was positively correlated with hatching date (Table 2.5, Figure 2.3). Without controlling for the other variables, hatch date and nest defence exhibited a significant positive linear correlation during the nestling stage ($r = 0.26$, $df = 73$, $p = 0.026$) but not during the egg stage ($r = 0.16$, $df = 70$, $p = 0.183$; Figure 2.3).

2.4 Discussion

With the exception of parental sex, I found no associations between the physical attributes of parent Mountain Bluebirds and their level of nest defence; rather, it was the stage of reproduction and number of offspring that seemed to drive the intensity of defence.

2.4.1 Nest Defence and Parental Attributes

Contrary to predictions from life-history theory, older parents did not defend more aggressively than yearling parents. The annual apparent survival rate for Mountain Bluebirds in central British Columbia has been estimated at 48% for both sexes and does not seem to vary with age (Johnson and Dawson 2020). Individuals may learn effective defence from successive encounters with predators (Montgomerie and Weatherhead 1988), but the relatively short lifespan of most bluebirds probably limits the amount of experience gained from past encounters with a nest predator. However, I was not able to accurately age adults older than 1 year based on molt (Pyle 1997), so it is possible that age effects only become apparent among the oldest individuals in the population. Because older males were more colourful and larger than yearling

males, I could not distinguish the affects of age per se from these other attributes. Regardless, no morphological characteristic was associated with aggressive behaviours towards a nest predator in my study.

Within each sex, I did not find the predicted relationship between body size or condition and defence level. The relatively small size difference among individuals may make little difference when defending against a mammalian predator larger than themselves. Mountain Bluebird parents were willing and able to invest in short term and energetically costly defensive behaviour in response to an acute threat to the nest, irrespective of their body condition. Fisher and Wiebe (2006) found similar results in Northern Flickers (*Colaptes auratus*). However, Hogstad (2005) noted positive correlations between defence and body condition for both sexes of Fieldfares (*Turdus pilaris*), whereas Hamer and Furness (1993) found that the aggression intensity of Great Skuas (*Stercorarius skua*) increased with body condition for females but decreased for males. This difference was attributed to sex roles in skuas where males do most of the foraging and maintain a low body mass to improve flight efficiency, whereas females are more sedentary near the nest and are able to accumulate more body reserves. In contrast to Great Skuas, male and female Mountain Bluebirds both provision nestlings, so the sexes may not maintain different fat stores on the body. Merkle and Barclay (1996) found that body mass in Mountain Bluebirds did not increase with food supplementation, which suggests that food is not limiting and that parents may adjust their foraging behaviour to regulate body reserves despite increased energy demands during the breeding season.

The hue of males, but not females, in my study shifted towards short-wavelength UV-blue with age, but I did not find any association between plumage colour and intensity of nest defence within either sex. In the same population of Mountain Bluebirds, plumage colour was

not associated with food delivery rates to nestlings (Stalwick and Wiebe 2019b). On a different study area in British Columbia, brighter Mountain Bluebirds with more UV-reflecting tails also did not provision more than duller parents (Morrison et al. 2014), so there is little support for the “good parent” hypothesis for plumage ornamentation in this species. More likely it functions as a cue of resource-holding potential among conspecific rivals for mates and territories as in Eastern Bluebirds (Mercadante and Hill 2014).

2.4.2 *Effects of Sex and Breeding Stage*

Males defended nests more aggressively than females during both breeding stages, which is counter to the paternity hypothesis. In other populations of Mountain Bluebirds, 63%–72% of broods contained at least one young from extra-pair mating by the female (Balenger et al. 2009, Johnson and Dawson 2020). While I have not measured extra-pair paternity in this population, it may be relatively low because most nests were spaced at least 1 km apart, potentially limiting contact between breeding pairs, but this needs further investigation.

Other studies have found that the larger sex defends more intensely in species of raptors where dimorphism ranges from 20% to 30% (e.g., Wallin 1987, Galeotti et al. 2000) and in Imperial Cormorants (*Leucocarbo atriceps*) where males are 18% larger than females (Svageļj et al. 2012). Among monogamous passerines in which males average 6% larger than females (Mills 2008), males defend more strongly in some species like Eurasian Nuthatches (*Sitta europaea*) (Nado et al. 2018) but not in others like Northern Cardinals (*Cardinalis cardinalis*) (Nealen and Breitwisch 1997). The degree of size dimorphism in Mountain Bluebirds is only about 1.7% (Johnson and Dawson 2020) and while consistent with the greater defence by males, body size does not appear to be the main driver of the intensity of nest defence in this species.

Constraints on renesting may explain the sex-related differences in the intensity of nest defence in my study. Experimentally widowed female Mountain Bluebirds found replacement partners more quickly than widowed males, suggesting that females may have a better renesting potential (Power 1975). Since males would have fewer reproductive alternatives if their mate died or disappeared, they may be more inclined than females to invest substantially in the current breeding attempt. The higher intensity of nest defence provided by males may also be due to their more consistent energy reserves (e.g., Merkle and Barklay 1996, Hogstad 2005). The energy costs of egg development may limit a female's ability to defend the nest during the incubation stage than later during the nestling stage when she is able to leave the nest more regularly to forage for herself (Merkle and Barclay 1996, Vifiddis et al. 2018). Because males do not form or incubate the eggs and provision slightly less than females during most of the nestling period (Stalwick and Wiebe 2019b), female bluebirds may be more energetically limited than males during most of the breeding period and less inclined to devote energy to offspring defence than the males during both stages.

Mountain Bluebirds of both sexes increased their defence from early (incubation) to late (nestling) breeding stages consistent with the idea that older offspring have greater survival prospects and are, therefore, of greater reproductive value to the parents (Montgomerie and Weatherhead 1988). The pattern is also consistent with the idea that as the time window for initiating a new clutch decreases, older offspring will be perceived as more valuable because they cannot be replaced, i.e., the renesting hypothesis. The seasonal increase in the intensity of nest defence cannot be explained by body condition, which actually declines during the season for both males and females (K.L. Wiebe, unpublished data). My study, among the first to test for an interaction between parental sex and breeding stage, also revealed that males escalated their

nest defence more than females as the breeding season progressed. This interaction could be similarly explained by the reneating hypothesis and the male's lack of future reproductive prospects compared to the female (e.g., Power 1975). The female may also be less willing to expend as much energy as the male during late breeding stages, if she is rebuilding her body reserves to lay a potential second clutch.

In contrast to the interaction between sex and stage of reproduction in my study, Hogstad (2005) observed that male, but not female, Fieldfares increased defence from the incubation to the nestling stage. He suggested that reneating costs were higher for female than males at the incubation stage because only females paid costs of building a new nest and laying eggs. However, it may be the opposite in cavity-nesting Mountain Bluebirds where, although the female brings grass to line a new nest, it is the male that must find and defend a new cavity (Power 1966), potentially on a new territory if the female relocates after nest loss. Securing a new cavity can come at considerable energetic cost against competitors (Wiebe 2016). Hence, male bluebirds, but not male Fieldfares, may be strongly invested in defending the current nest location early in the breeding cycle. Furthermore, the body condition of female, but not male, Fieldfares decreased between the incubation stage and the nestling stage, so energy reserves may be more of a limiting factor in defence by Fieldfares compared to bluebirds.

2.4.3 Effects of Seasonal Timing and Size of the Brood

Within each breeding stage and while controlling for age of the offspring, defence levels increased with the hatch date of the clutch consistent with the reneating hypothesis. Defence levels likely did not decline for the latest broods in my study because even in late broods, nestlings had ample time to fledge, did not appear to be malnourished, and hence still had high reproductive value. Consistent with parental investment theory, the level of defence generally

correlated positively with brood size, which has also been reported in other bird species such as the Imperial Cormorant (Svigelj et al. 2012) and various passerines (Knight and Temple 1986, Curio and Regelman 1987). A greater sample size of Mountain Bluebirds with fewer than five eggs is needed to determine accurate defence levels for the smallest broods. Although Mountain Bluebird parents seemed to adjust defence according to the number of offspring, other studies have found no such relationship (Fisher and Wiebe 2006, Redmond et al. 2009). A positive correlation between the intensity of nest defence and the number of offspring may also reflect the general quality of the parents (Curio and Regelman 1987, Svigelj et al. 2012). To tease apart these effects, brood size manipulation experiments are needed, such as those performed in Tryjanowski and Golawski (2004).

In summary, features of the brood itself (size, hatch date, and breeding stage) were associated with the intensity of nest defence of Mountain Bluebirds more than the physical attributes of the parents, and the greater defensive effort by males compared to females seems most consistent with the reneating hypothesis.

Table 2.1. Principal Component axis loadings for the seven measures of nest defence. Data are from 51 male and 54 female Mountain Bluebirds assessed while interacting with a model squirrel predator during 5 min trials during the incubation and nestling stages.

Variable	PCA axis		
	1	2	3
Average Distance (Log)	0.789	0.247	0.428
Dives (Log)	0.883	-0.251	-0.202
Hits (Log)	0.873	-0.405	-0.005
Dive Distance (Log)	0.733	-0.571	0.088
Hover Time	0.749	0.487	-0.326
Aggressive Time	0.907	0.21	-0.271
Latency Time (Log)	0.787	0.309	0.345
Variation explained (%)	67.2	14.14	7.59

Table 2.2. Principal Component axis loadings for the 3 measures of remige colour for each sex (41 males and 40 females). The colour variables were extracted from spectrometer measurements.

Variable	PCA axis (males)		PCA axis (females)	
	1	2	1	2
Brightness	0.257	0.954	0.606	0.787
Hue	-0.899	-0.035	0.964	-0.056
Chroma (blue or UV)	0.850	-0.325	-0.837	0.505
Variation explained (%)	53	34	67	29

Table 2.3. General linear models (LM) testing the effect of morphological attributes including plumage colour PCA score on nest defence intensity of male Mountain Bluebirds. Separate models were run for each age class at the two stages of breeding. The coefficient estimates (unstandardized) and standard errors were obtained using the “summary” function in R and the degrees of freedom, *F*, and *p* values were obtained using the “Anova” function.

Breeding Stage	Independent variable	Yearling male				Adult male			
		Coefficient	df	<i>F</i>	<i>p</i>	Coefficient	df	<i>F</i>	<i>p</i>
Incubation	Condition	-0.38 ± 0.52	1,7	0.53	0.53	-0.18 ± 0.16	1,16	1.34	0.26
	Size	-0.12 ± 0.85	1,7	0.02	0.89	-0.22 ± 0.26	1,16	0.73	0.41
	PC1	0.19 ± 1.31	1,7	0.02	0.89	0.34 ± 0.42	1,16	0.65	0.43
Nestling	Condition	-0.20 ± 0.48	1,6	0.17	0.69	-0.15 ± 0.14	1,19	1.11	0.30
	Size	0.13 ± 0.79	1,6	0.03	0.87	-0.32 ± 0.21	1,19	2.35	0.14
	PC1	-0.38 ± 1.31	1,6	0.08	0.78	0.34 ± 0.35	1,19	0.96	0.34

Table 2.4. General linear models (LM) testing the effect of morphological attributes on nest defence intensity of female Mountain Bluebirds. The coefficient estimates (unstandardized) and standard errors were obtained using the “summary” function in R and the degrees of freedom, F , and p values were obtained using the “Anova” function.

Breeding stage	Independent variable	Coefficient	df	F	p
Incubation	Female age	-0.09 ± 0.30 (mature)	1,31	0.09	0.78
	Body condition	-0.10 ± 0.08	1,31	1.60	0.22
	Body size	-0.21 ± 0.19	1,31	1.23	0.28
	Colour PC1	0.10 ± 0.14	1,31	0.51	0.48
Nestling	Female age	-0.24 ± 0.36 (mature)	1,30	0.45	0.51
	Body condition	-0.15 ± 0.09	1,30	3.00	0.09
	Body size	0.08 ± 0.22	1,30	0.12	0.73
	Colour PC1	0.23 ± 0.19	1,30	1.46	0.23

Table 2.5. Linear mixed model (LMM) analyzing the effect of parental sex and traits of the brood on the nest defence score of Mountain Bluebirds. Coefficient estimates (unstandardized) were obtained using the “summary” function in R and the degrees of freedom, *F*, and *P* values were obtained using the “Anova” function.

Fixed effects	Coefficient ± SE	df	<i>F</i>	<i>P</i>
Sex	0.71 ± 0.20 (male)	1,71	9.12	0.004
Stage	-0.52 ± 0.10 (incubation)	1,69	85.3	<0.001
Brood size	0.25 ± 0.10	1,71	4.59	0.04
Hatch date	0.06 ± 0.02	1,71	6.68	0.01
Sex*Stage	-0.31 ± 0.15	1,69	4.54	0.04

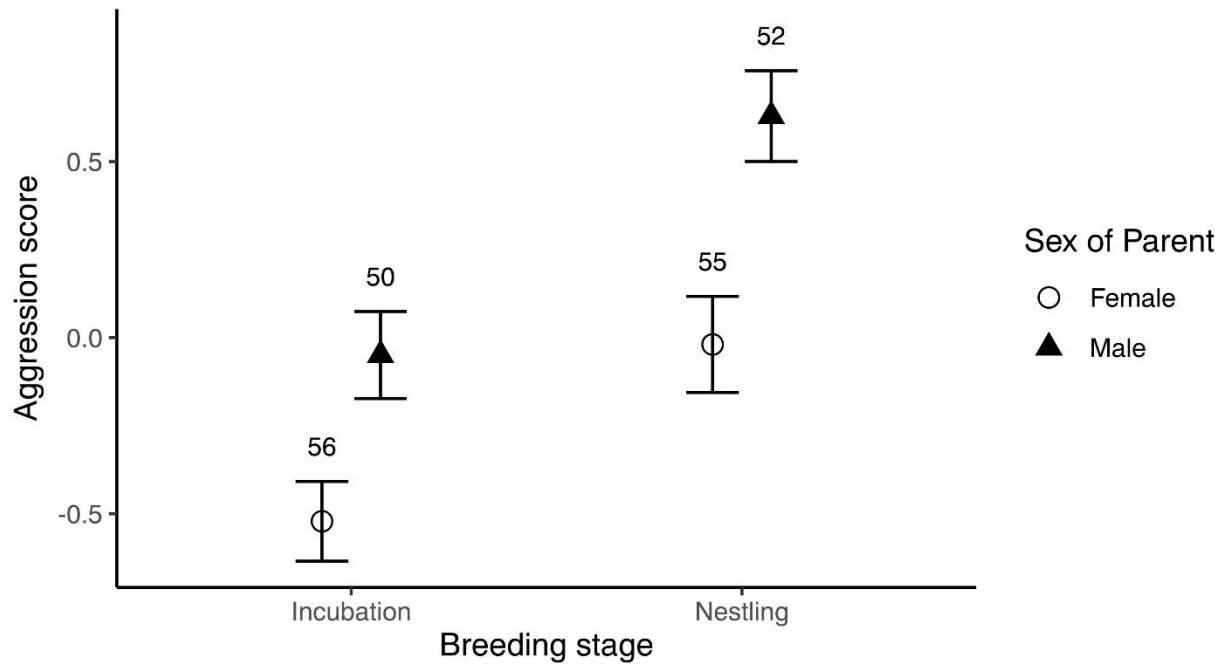


Figure 2.1. Nest defence intensity (PCA aggression score) of Mountain Bluebirds according to breeding stage and sex of the parent (circle=female, triangle=male). Means \pm SE are shown with sample sizes above the bars.

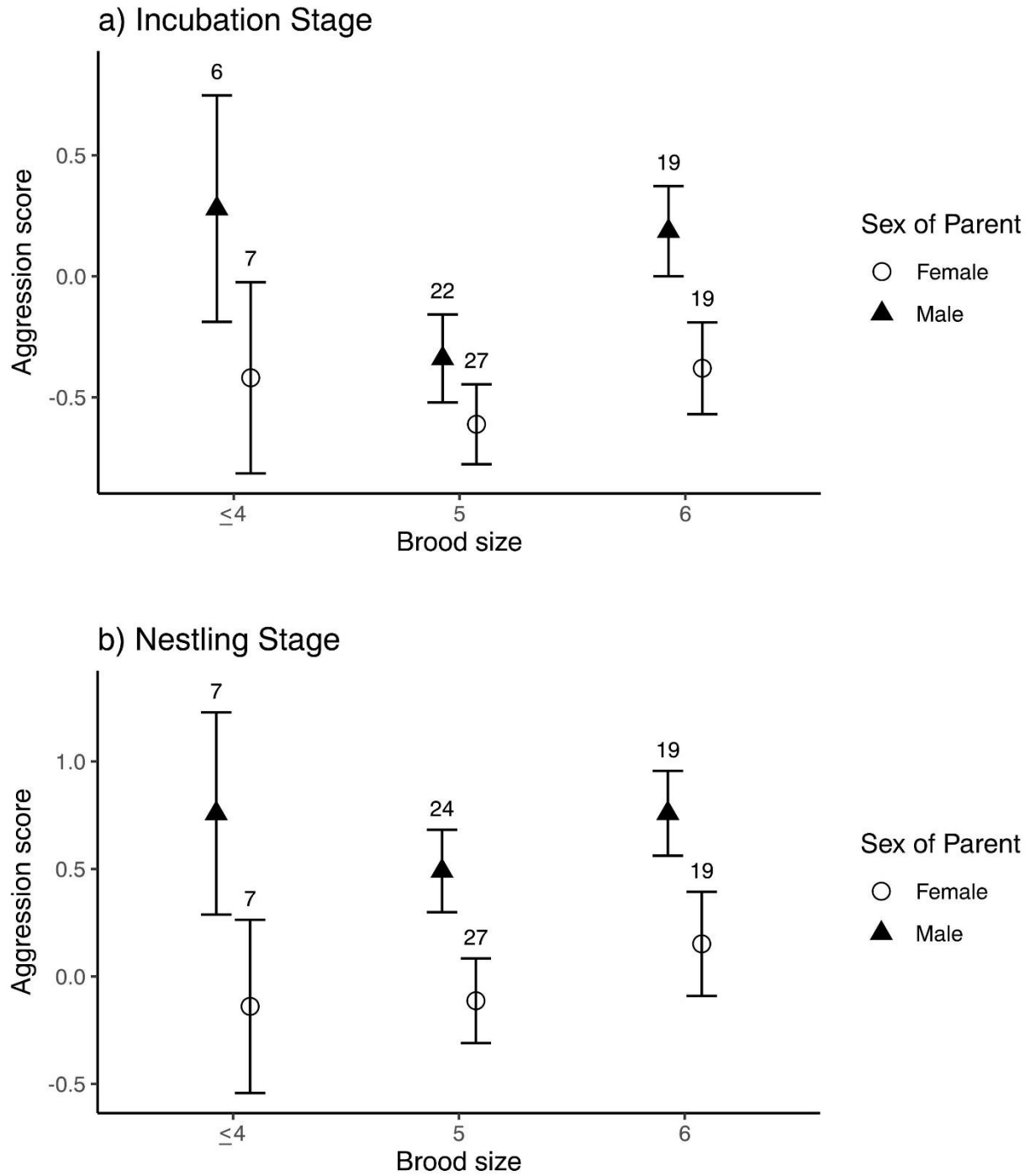


Figure 2.2. Nest-defence intensity (PCA aggression score) of Mountain Bluebirds according to brood size and sex of the parent (white circle=female, black triangle=male). Aggression was measured during the incubation stage (a) and nestling stage (b). Means \pm SE are shown with sample sizes above the bars.

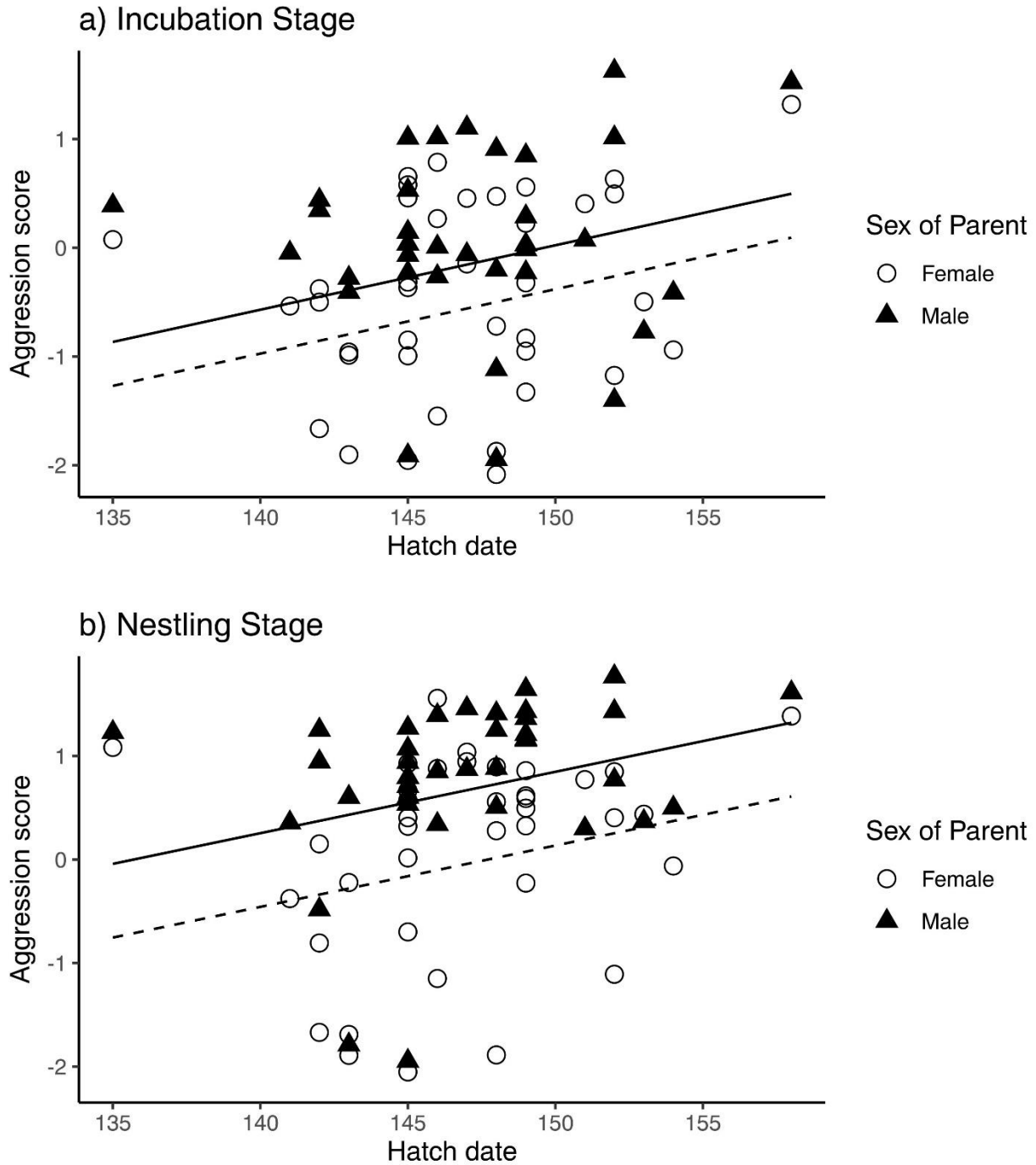


Figure 2.3. Relationship between aggression of male and female mountain bluebirds (dashed line=females, solid line=males) defending their brood against a model nest predator and the hatch date (1 = 1 January) of the offspring. Aggression was measured during the incubation stage (a) and nestling stage (b).

CHAPTER 3: INCUBATION RHYTHMS OF MOUNTAIN BLUEBIRDS IN RESPONSE TO PREDATION RISK

3.1 Introduction

The risk of predation has a diverse effect on a range of behaviours in birds such as foraging (Abdulwahab et al. 2019), nest site selection (Forstmeier and Weiss 2004) and provisioning offspring (Ghalambor et al. 2013). Less well-studied are the potential effects on incubation behaviour caused by the immediate threat of predation (Basso and Richner 2015). One hypothesis, first proposed by Skutch (1949), suggests that parental visits to the nest draw the attention of predators to the nesting site. This may lead females in situations of high predation risk to minimize recess rates to foraging for themselves during incubation (Skutch 1962). This could lead to greater total time on the eggs (high incubation constancy), potentially at a cost to the energy balance of incubating females (Skutch 1962). Alternatively, the female may prioritize her own survival, and so after experiencing a predation attempt may be more wary and flush more easily in response to noises and disturbance near the nest. As a result, the number and length of periods the female is off the nest (i.e., incubation recesses) might increase.

Skutch's hypothesis has been tested in several species; for example, Basso and Richner (2015) found that female Great Tits (*Parus major*) exposed to a stuffed short-tailed weasel (*Mustela erminea*) throughout the incubation period had an overall reduction in recess rates. However, few studies have looked at the recovery time immediately following exposure to a nest predator. Research by Zanette et al. (2011) on Song Sparrows (*Melospiza melodia*) indicates that even the perception of predation risk will reduce the number of offspring produced in the same year by as much as 40%. This may imply that incubating parents continue to feel threatened after the immediate threat has passed because of they perceived that the predator was still present.

Incubating females will likely feel pressured to return to normal incubation patterns as soon as possible but may also be very cautious about the nest predator returning (Morosinotto et al. 2013). Therefore, a female's willingness to return to normal incubation patterns may be related to the temperature fluctuations caused by the ambient temperature outside the nest as well as her own morphological and behavioural traits.

The ambient temperature outside the nest has been shown to influence energy expenditure of incubating birds (Haftorn and Reinertsen 1985, Tinbergen and Williams 2002, Cresswell et al. 2004). A lower ambient temperature requires birds to increase their time on the nest to ensure that temperature does not fluctuate too much and prevent their eggs from developing properly (Webb 1987, Matysioková and Remeš 2010). Although developing embryos are able to withstand some temperature fluctuations and periods of chilling, prolonged exposure to low temperatures may cause developmental problems or hatching failure (Webb 1987). An increased risk of nest predation may increase these fluctuations if the female is more cautious about spending more time on the nest. Alternatively, a female's incubation constancy may increase if she spends more time on the nest to potentially limit exposing the nest to predators.

An important aspect of reproductive success in many bird species is the variation in investment associated with age, with older females spending more time incubating the eggs (Stutchbury and Robertson 1988, Yerkes 1998, Ardia and Clotfelter 2007). One possible explanation for age affecting incubation could be that older females are generally more efficient at finding food for themselves (Wunderle 1991). Older and more experienced females are also more likely to choose better quality habitats (Amininasab et al. 2016) which may reduce foraging time needed and leaves the female more time to prioritize incubation.

Throughout the breeding season, individuals face a trade-off between maintaining their body condition and reproductive effort (Mitchell et al. 2012). Birds with higher body condition are more attentive to their clutch (higher constancy) than individuals with lower body condition (Gatti 1983, Gorman and Nager 2003), possibly because they require less foraging time to maintain their body reserves. Constraints on incubation constancy are especially true in bird species where the female is the only parent that incubates the eggs and is under more stress to maintain a balance between her physical and reproductive fitness (Tinbergen and Williams 2002, Conway and Martin 2000). For example, Wiebe and Martin (1997) found that female White-tailed Ptarmigan (*Lagopus leucurus*) took significantly more recesses of longer duration during a breeding season when body condition was lower. Thus, under the risk of predation, female birds with higher body reserves may be in a better position to limit the number of recesses and the duration of each recess so as to avoid attracting the attention of a predator.

Active defence of nests against predators is a way that parents may improve the survival of their offspring (Svagej et al. 2012) and some studies show that the intensity of defence is positively correlated with offspring survival (Andersson et al. 1980, Knight and Temple 1986, Tryjanowski and Goławski 2004). Although a few studies have shown that birds alter incubation rhythms in response to predation risk, most have not examined the potential relationship between the physical aggressiveness of nest defence and incubation behaviour. If high levels of aggression towards a predator successfully deter future attacks (Blancher and Robertson 1982), I predict that aggressive females will alter their incubation behaviour less after an encounter with a predator relative to non-aggressive females.

To understand the predation risk-incubation trade-off more broadly, I exposed incubating Mountain Bluebirds (*Sialia currucoides*) to a model of an american red squirrel (*Tamiasciurus*

hudsonicus), the primary nest predator in the study area (Stalwick and Wiebe 2019a). I recorded the control incubation behaviour (constancy, recess length, and recess rate) before exposure to the predator and examined incubation responses in relation to a broad range of factors including morphological traits of the female (age, body condition), a behavioural trait (aggression towards nest predator), as well as the ambient temperature surrounding the nest. I was unaware of any study examining how incubation behaviour potentially recovers following a single exposure to a nest predator, so I compared incubation rhythms prior to predator exposure to those one, two, and three days following predator exposure.

In keeping with Skutch's (1949) hypothesis that lowering the activity around the nest site will reduce its detection by predators, I predict that recess rate will decrease after exposure to a model nest predator while recess length will increase as females try to recoup energy during fewer, but longer breaks from the nest. As a result, I also predict overall constancy will increase. Anticipating that older females and those with higher body condition will spend more time on their nests (Gorman and Nager 2003, Ardia and Clotfelter 2007), I predict that constancy will be positively associated with age and body condition whereas recess rate and length will decrease. I also predict that incubation behaviour will not vary as much from before and after exposure to a model predator in higher quality females (i.e., older, more aggressive, and higher body condition) than in lower quality females. Finally, I predict that constancy will increase as ambient temperature decreases and that recess rate and/or length will decrease as ambient temperature decrease.

3.2 Materials and Methods

3.2.1. Study Site and Species

The Mountain Bluebird is an insectivorous cavity-nesting thrush weighing roughly 30 g that breeds throughout northwestern North America in grasslands, clear-cuts, and burns (Johnson and Dawson 2020). This study was conducted in central British Columbia from April-June 2019 near Bridge Lake (51° 28' N, 120° 43' W, 1140 m a.s.l.) and 100 Mile House (51° 38' N, 121° 17' W, 970 m a.s.l.). More than 300 plywood nest boxes were placed on retained trees in logging cuts and on fence posts in grazed grasslands (see Stalwick and Wiebe 2019a). Mountain Bluebirds typically arrive on these study areas after migration around mid-March and lay clutches of 5 to 6 eggs on average (Stalwick and Wiebe 2019b). Only females incubate (Johnson et al. 2013a). Once the nestlings hatch, both sexes provision the offspring with a variety of invertebrate prey (Power 1980, Herlugson 1982, Stalwick and Wiebe 2019b), and the nestlings fledge after 15-22 days (Johnson et al. 2013b).

3.2.2 Field Methods

While provisioning their young (between nestling ages 3-13 days), females were trapped in the nestbox using a swing-door trap. Each was banded with a unique combination of a single Canadian Wildlife Service numbered aluminum band and 3 colour bands for future identification and aged as either a yearling or a mature adult (>1 yr) based on molt of the secondary coverts (Pyle 1997). Captured females ($n = 34$) were weighed and 6 measures of structural size were taken: length of the combined head and bill length, culmen, tarsus, central rectrix, 10th primary flight feather, and flattened wing chord. I entered these measures in a principal component analysis, using the score on the first axis (PC1) as a measure of overall body size (Rising and

Somers 1989). A body condition index was then calculated using the residuals from a regression of body mass on PC1 as in Labocha and Hayes (2012) and Wiebe and Vitousek (2015).

3.2.3 Predator Experiment

When near the nest box (but not inside it), a red squirrel poses a risk to the nest contents but not to parents (Stalwick and Wiebe 2019a). I placed the predator model on the roof of the nest box of 34 Mountain Bluebird pairs during the incubation stage 4-6 days after the last egg had been laid. Reactions to the model were recorded by an observer concealed in a small camouflage blind placed about 40 m from the nest box and by a video camcorder (Panasonic HDC-SD80) placed on a tripod about 5 m from the nest box. When at least one parent appeared within sight of the box (i.e., within 50 m), a fishing line attached to a small cloth that covered the squirrel was pulled to reveal it and parental responses were recorded for 5 min before taking the model away. From the videos, I extracted 7 variables related to the intensity of defence: (1) distance of the parent from the model predator, measured every 15 s and then averaged (Average Distance), (2) the number of dives at the model (Dives), (3) the distance between the parent and the model predator during a dive (Dive Distance), (4) the number of hits on the model (Hits), (5) the duration of time hovering near the model (Hover Time), (6) the total time during the trial spent on any active aggression (e.g., hovering, flying, diving) towards the model (Aggressive Time), and (7) the time lag from when the model was revealed to when a parent first reacted to the model (Latency Time). I used a principal component analysis (PCA) to extract a single aggression score from the PC1 axis loadings of these six variables (see also Olendorf and Robinson 2000, Quesada and Senar 2007). For details on the aggression scores see (Tkaczyk et al. 2022).

Because the predator trials also involved a human visiting the nest box, I cannot interpret the female's subsequent response during incubation as solely in reaction to the squirrel versus to a level of increased risk that was associated with a combination of squirrel model presence and human disturbance.

3.2.4 Incubation Data Collection

Temperature in nest bowls ($n = 42$) was recorded using iButtons (Maxim Integrated; <https://www.maximintegrated.com/en.html>) to detect the timing and length of incubation recesses. The iButtons were fastened to a wire, which was threaded through the nest material and secured to the bottom of the nest box to prevent females from moving them (Johnson et al. 2013a, Walters et al. 2016, Stalwick and Wiebe 2019a). Direct observations of some incubating females in a previous study confirmed that absences from the nest corresponded well with traces recorded by iButtons (Stalwick and Wiebe 2019a). The ambient temperature was recorded during the same time as the iButtons in the nests using a separate iButton attached to the outside bottom of nest boxes (see Walters et al. 2016). When multiple nest boxes were located within about 5 km of each other and predator trials at the boxes occurred on the same day, a single ambient temperature reading was used for all boxes. All iButtons were set to record temperature every 3 minutes at a resolution of ± 0.5 °C.

I placed iButtons in the nests about 4 days after clutch completion and let them run for about two days (49.3 hours ± 0.57) to collect control data on incubation rhythms. After this control period, I conducted the predator trial with the squirrel model. Immediately after the trial, I placed new iButtons inside and outside the nest for additional monitoring that lasted 51.5 hours ± 0.82 to record any shifts in the incubation rhythms.

3.2.5 Incubation Rhythm Data

The iButton data were categorized as either pre-trial (control) or post-trial. The first 8 temperature measurements (approximately 24 minutes) from both periods were discarded to allow the female to return to the nest and the iButton to adjust to the nest temperature. Pre-trial (control) data were averaged over that period. Because I was interested in the duration of any responses after predator exposure, I divided the post-trial period into three sub-periods corresponding to the 3 days after the predator trial. Since trials were normally conducted in the morning, period 1 included the time immediately after predator exposure to the final recess that day before the female stayed in the box overnight. Periods 2 and 3 each included the first recess in the morning that day to the final recess before nightfall.

I initially identified the beginning of a recess (period off the nest) as any time the temperature dropped by least 1.5 °C over a 3-minute period, and the end of a recess was similarly marked when the temperature increased by least 1.5 °C over a 3-minute period (Walters et al. 2016). I then visually inspected plots of both the nest and ambient temperature data (Figure 3.1) to confirm that any subtle dips in nest temperature had not been missed when the ambient temperature was high (e.g. > 25 °C). For each of the four time periods (pre-trial (control), 3 post-trial), I then calculated the percentage of daylight hours spent on the nest (constancy), the average recess length, and the recess rate (number of recesses/ hour). I also calculated the average ambient temperature during the daylight hours (corresponding to the period from dawn to dusk when the incubation behaviour was recorded) for each time period.

3.2.6 Statistical Analyses

In a preliminary analysis, I used General Linear Models (“lm” function in R version 3.6.1, R Core Team 2019) to test whether the hour of day the predator trial took place (period 1)

influenced any of the three incubation variables. Because there was no relationship with constancy ($F_{40} = 0.22$, $P = 0.64$), recess length ($F_{40} = 0.21$, $P = 0.65$), and recess rate ($F_{40} = 0.12$, $P = 0.73$), I did not include time of day in subsequent models. For the control period prior to predator exposure, I used General Linear Models to examine effects of several independent variables (female age, female body condition, and average ambient temperature) on each of the three continuous dependent variables (Constancy, Recess Length, and Recess Rate). Significance was set at $P < 0.05$ and was calculated using Type III sums of squares with the “Anova” function from the “car” package (Fox and Weisberg 2019). Not all females could be captured at all nests, so this set of models was done with a smaller sample size ($n = 34$) than the total number of trials conducted. Of the three dependent variables, constancy and recess rate were normally distributed. However, recess length was positively skewed and so an inverse transformation was applied to that variable before analysis. To normalize the distribution of the ambient temperature, a log transformation was applied before analysis.

To examine effects of the predator exposure, I used repeated measures linear mixed-effects models (LMMs) for each incubation variable using the “lmerTest” package (Kuznetsova et al. 2017). For each model, I entered the aggression score of the female and the average ambient temperature from each time period as covariates. The degrees of freedom for these models were rounded because they are the calculated estimates. To examine differences between the four time periods, I calculated estimated marginal means (EMMs) from the LMM models for the three dependent variables using the “emmeans” package (Searle et al. 1980). These models were created using then “lm” function in R version 3.6.1 (R Core Team 2019).

3.3 Results

During the control (pre-period), average ambient daily temperatures varied from 10.2 °C to 24.2 °C, averaging $14.1 \text{ °C} \pm 0.48 \text{ SE}$. The GLMMs indicated that female age, body condition, and ambient temperature did not affect recess length, recess rate, or constancy before exposure to a nest predator (Table 3.1). The mean recess length during the pre-trial period was $11.4 \text{ min} \pm 0.22$, the mean recess rate was $2.33/\text{hour} \pm 0.05$ and the mean constancy was $57.2\% \pm 0.007$.

The repeated-measures analyses which examined changes in the incubation variables across the four time periods revealed significant shifts in all three incubation variables in response to the predator model (Table 3.2). The post-hoc contrasts to determine which periods differed significantly from one another (Table 3.3) showed that immediately after the trial (in period 1), recess rates declined (Figure 3.2), recess lengths increased (Figure 3.2) and constancy declined but only marginally so (Figure 3.2). By the day following the predator trial (period 2), recess rate and length still differed from the control period whereas the constancy did not (Table 3.3). By the second day after exposure to the predator, in period 3, none of the incubation variables differed from the control (pre-trial) state.

The intensity of aggression by the female parent against the model squirrel was not associated with any of her subsequent incubation responses (Table 3.2). There was a negative relationship between ambient temperature and constancy (Table 3.2, Figure 3.3) but no significant effect of ambient temperature on recess rate or length.

3.4 Discussion

The incubation response by female bluebirds was not influenced by a female's physical or behavioural attributes. While the incubation responses were not affected by ambient

temperature before exposure to a predator, incubation constancy was affected by the ambient temperature after the predator trial possibly because of a larger sample size.

3.4.1 Changes in rhythms immediately after exposure

Consistent with the hypothesis that females reduce activity at nests to avoid drawing the attention of predators to its location (Skutch 1949), incubating female Mountain Bluebirds reduced recess rates by about 31% immediately following the exposure to a model of an american red squirrel. Several other studies in birds have documented declines in recess rates after exposure to simulated predation risk. For example, Ibáñez-Álamo and Soler (2012) found that incubating female Common Blackbirds (*Turdus merula*) significantly reduced the number of visits to their nests by 29% after exposure to calls of a nest predator, the Eurasian Magpie (*Pica pica*), and Basso and Richner (2015) found that Great Tits reduced their recess rate by 19% after exposure to a stuffed short-tailed weasel.

Assuming that most of the time away from the clutch is dedicated to foraging to maintain energy intake during incubation, a female probably must increase the length of recesses if she decreases their number. Indeed, I found evidence of this potential trade-off in incubation rhythms because average recess length in Mountain Bluebirds increased after exposure to the predator. Kovařík and Pavel (2011) also found that the recess length of incubating female Meadow Pipits (*Anthus pratensis*) increased by roughly 31% in the presence of a nest predator (a stuffed magpie) relative to controls. Evidence for this potential trade-off was also demonstrated by Vafidis et al. (2018) who found that food-supplemented incubating Eurasian Reed Warblers (*Acrocephalus scirpaceus*) had shorter recess lengths than unsupplemented birds, possibly because the former could forage for a shorter time and over shorter distances.

A combination of both recess number and recess length will determine total incubation constancy. That constancy declined but only weakly so ($p = 0.06$) on the day of exposure to the predator shows that the reduced number of recesses was largely offset by longer recess length. Constancy increased over the 3 days following exposure to the predator but never differed significantly from control values. Thus, female Mountain Bluebirds seem to place a high priority on regulating the temperature of the eggs even during the threat of nest predation. The average constancy in this study was similar to the 61% constancy found in the closely related Eastern Bluebirds (*Sialia sialis*) (Pinkowski 1979).

3.4.2 Duration of the anti-predator response

Incubation behaviour, specifically the average recess rate and length, returned to pre-trial levels two days after the predator trial. This may indicate that females are under pressure to return to normal recess behaviours quickly to maintain optimal incubation temperatures (Haftorn 1988). Failing to resume a high constancy may have severe fitness consequences. For example, the eggs of Zebra Finches (*Taeniopygia guttata*) that were periodically cooled had smaller embryonic mass compared to those incubated at a constant temperature (Olson et al. 2008). In general, the energetic costs of incubation are expected to increase when female birds must rewarm very cold eggs (Vleck 1981). Therefore, it may be the most efficient in the long term to prevent the eggs from cooling too much by keeping recess lengths short, and this may require more frequent recesses. Female Mountain Bluebirds are apparently willing to sacrifice incubation efficiency in the short term when faced with the risk of a predator near the nest but return to normal incubation behavioural patterns a day later if there is no further disturbance.

I also found that constancy increased during the second and third day after predator exposure; perhaps the female tried to compensate for somewhat reduced constancy immediately

after exposure to the predator. Basso and Richner (2015) found that incubation constancy of Great Tits was not significantly affected by exposure to a nest predator over the course of the nesting season. However, to the best of my knowledge, this is the first study to measure constancy immediately following a predator trial.

3.4.3 Influence of ambient temperature and individual traits on incubation

As predicted, constancy decreased as ambient temperature increased in post-trial time periods. In cold weather, egg temperature declines more rapidly when the female leaves for a recess and so long absences risk optimal embryo growth (Webb 1987, Olson et al. 2008). A negative correlation between constancy and ambient temperature seems to be a common pattern in passerine birds such as Pied Flycatchers (*Ficedula hypoleuca*) (Sanz 1997), Great Tits (Matysioková and Remeš 2010), and Eurasian Blue Tit (*Cyanistes caeruleus*) (Amininasab et al. 2016). This suggests that females regulate their time on the nest according to even small fluctuations in the outside temperature in a way that optimally trades-off foraging with warming the embryos (Vafidis et al. 2018). However, I found no association between the ambient temperature and recess rate and length either before or after the predator trial. Thus, it seems that trade-offs between the length and the number of recesses allow the behavioural flexibility required to minimize detection of the nest when it is directly threatened (Conway and Martin 2000).

The incubation rhythms (Constancy, Recess Length, and Recess Rate) of Mountain Bluebirds were not associated with age or body condition of the female. Although breeding variables such as laying date, clutch size and fledging success improve with age across many species (Martin 1995, DeForest and Gaston 1996, Goutte et al. 2010), information on age-related incubation is more scant (Yerkes 1998, Bogdanova et al. 2007). Perhaps successful incubation

rhythms are so tightly constrained by the need to maintain relatively constant temperatures that there is little room for improvement with experience. A relationship with the body reserves of females and incubation rhythms have been documented in larger-bodied capital breeders such as waterfowl and galliformes. For example, Mallards (*Anas platyrhynchos*) (Gatti 1983) and Wood Ducks (*Aix sponsa*) (Hepp et al. 2005) in good condition had higher constancy, and White-tailed Ptarmigan in good condition had fewer recesses (Wiebe and Martin 1997), probably because higher body reserves reduced the need for foraging. Body condition may be less relevant for “income breeders” like small passerines. Female Mountain Bluebirds also benefit from some incubation-feeding by their mates (Johnson and Dawson 2020) which could mediate the potential trade-off between body condition and the number and length of recesses.

In contrast to my predictions, I found no evidence that females that were more aggressive towards a nest predator showed less of a response in incubation behaviour immediately following a predator trial. Apparently, once the nest predator leaves the vicinity of the nest, females are simply motivated to resume normal incubation behaviour.

In summary, incubating females reacted to an acute predation threat at the nest by minimizing activity at the site as predicted, and compensated by increasing the length of recesses. However, the shift in incubation rhythm was short-lived, persisting only two days after exposure and returning to normal after that. This is one of the first studies to investigate the length of the incubation response to an encounter with a predator. Currently, little is known about how fluctuations in incubation patterns caused by predation risk are influenced by egg mass and clutch size (Ibáñez-Álamo et al. 2015). The presumed greater demand associated with a larger egg and clutch size may influence these fluctuations in passerines. In addition, most predation research has been conducted during daylight hours despite nest predation still

occurring after dark (Weidinger 2010). Such questions could be looked into using this study and its findings as a framework for future research.

Table 3.1. General linear models testing the relationship between the independent variables (age of the female parent, female body condition, and average ambient temperature) and the three dependent incubation variables (Constancy, Recess Length, Recess Rate) for Mountain Bluebirds during the pre-trial period. Each variable’s coefficient estimates (unstandardized) were obtained using the “summary” function in R. The degrees of freedom, F, and P values were obtained using Type III sums of squares with the “Anova” function from the “car” package in R.

Dependent Variables	Fixed Effects	Coefficient \pm SE	df	F-value	P-value
Constancy	Age	-0.011 \pm 0.009	1,29	1.492	0.232
	Body Condition	-0.003 \pm 0.004	1,29	0.541	0.468
	Ambient Temp	0.001 \pm 0.003	1,29	0.224	0.640
Recess Length	Age	0.0009 \pm 0.001	1,29	0.371	0.547
	Body Condition	0.0005 \pm 0.001	1,29	0.550	0.464
	Ambient Temp	-0.0005 \pm 0.0005	1,29	1.075	0.308
Recess Rate	Age	0.089 \pm 0.056	1,29	2.493	0.125
	Body Condition	0.026 \pm 0.027	1,29	0.934	0.342
	Ambient Temp	-0.018 \pm 0.019	1,29	0.886	0.354

Table 3.2. Linear mixed models (LMMs) in a repeated measures design which compares the three dependent variables across the four time periods (pre-trial period and 3 periods (days) after exposure to the predator). Significant P-values from the models are bolded. Degrees of freedom are rounded estimates. The coefficient estimates (unstandardized) were obtained using the “summary” function in R. The degrees of freedom, F, and P values were obtained using Type III sums of squares with the “Anova” function from the “car” package in R.

Dependent Variables	Fixed Effects	Coefficient \pm SE	df	F-value	P-value
Constancy	AggressionPCA	0.010 \pm 0.009	1,36	1.254	0.270
	Ambient Temp	-0.002 \pm 0.001	1,117	11.214	0.001
	Period	-0.008 \pm 0.002	1,110	7.950	<0.001
Recess Length	AggressionPCA	-0.0003 \pm 0.001	1,36	0.050	0.825
	Ambient Temp	-0.00002 \pm 0.0001	1,122	0.026	0.872
	Period	-0.009 \pm 0.0004	3,111	127.873	<0.001
Recess Rate	AggressionPCA	-0.069 \pm 0.056	1,36	1.520	0.226
	Ambient Temp	0.001 \pm 0.002	1,114	0.260	0.611
	Period	-0.212 \pm 0.010	3,110	125.029	<0.001

Table 3.3. Estimated marginal means (EMMs) testing the significance of any difference between the four time periods in the three LMM models (one for each of the dependent variables). Coefficients are estimated marginal means \pm SE. Significant P-values from the models are bolded. All values were obtained using the “emmeans” package in R.

Period	Fixed Effects	Coefficient \pm SE	t-ratio	P-value
Constancy	Pre-Post1	-0.010 \pm 0.004	-2.506	0.064
	Pre-Post2	-0.006 \pm 0.004	-1.655	0.352
	Pre-Post3	0.008 \pm 0.004	2.358	0.091
	Post1-Post2	-0.004 \pm 0.004	-1.033	0.730
	Post1-Post3	-0.018 \pm 0.004	-4.563	<0.001
	Post2-Post3	-0.014 \pm 0.004	-3.921	<0.001
Recess Length	Pre-Post1	-0.013 \pm 0.0007	-17.562	<0.001
	Pre-Post2	-0.002 \pm 0.0007	-3.648	0.002
	Pre-Post3	-0.0007 \pm 0.0007	-1.026	0.734
	Post1-Post2	-0.010 \pm 0.0007	-15.122	<0.001
	Post1-Post3	-0.012 \pm 0.0007	-16.310	<0.001
	Post2-Post3	-0.002 \pm 0.0007	-2.613	0.049
Recess Rate	Pre-Post1	-0.299 \pm 0.018	-16.925	<0.001
	Pre-Post2	-0.051 \pm 0.016	-3.110	0.013
	Pre-Post3	0.002 \pm 0.016	0.111	1.000
	Post1-Post2	-0.248 \pm 0.017	-15.01	<0.001
	Post1-Post3	-0.301 \pm 0.018	-16.693	<0.001
	Post2-Post3	-0.053 \pm 0.017	-3.182	0.010

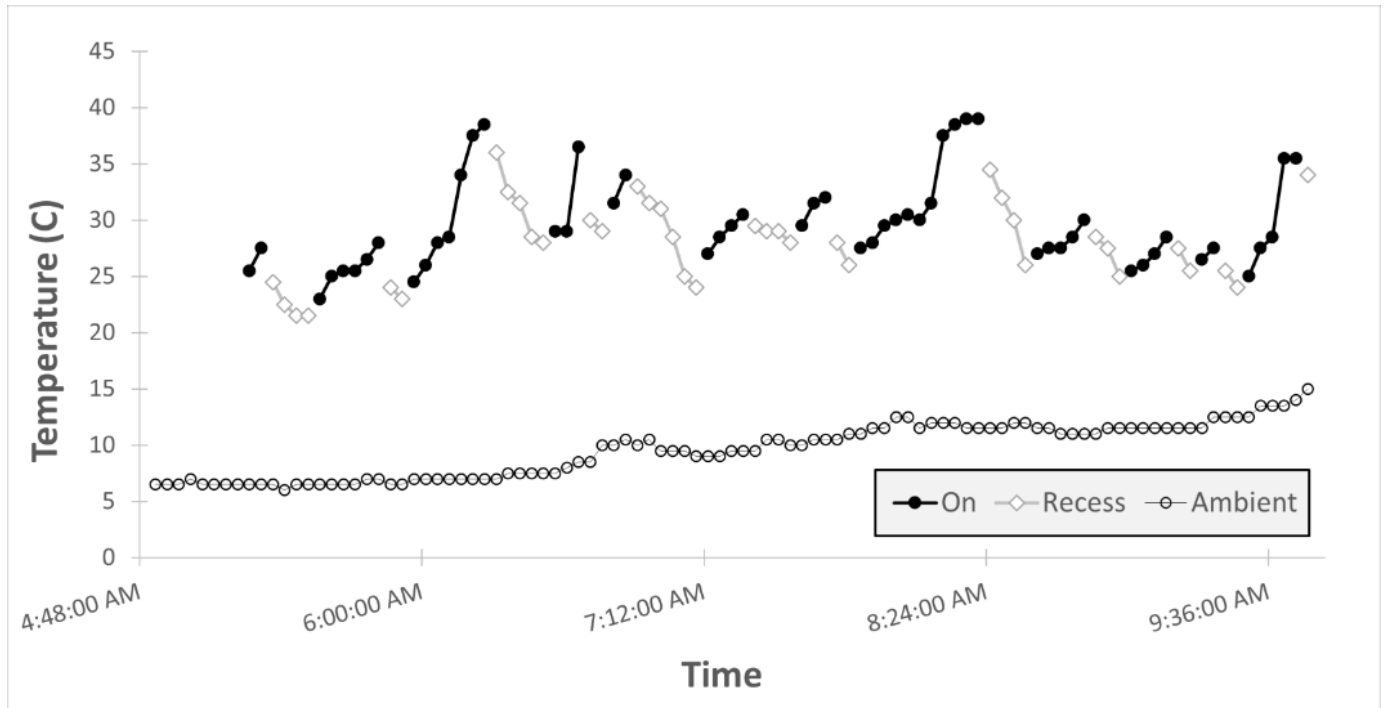


Figure 3.1. Example of raw temperatures measured every 3 minutes by an iButton placed in the nest cup of a Mountain Bluebird and one placed outside and below the box. Periods when the bird is incubating “on” the eggs versus taking a recess away from clutch are shown.

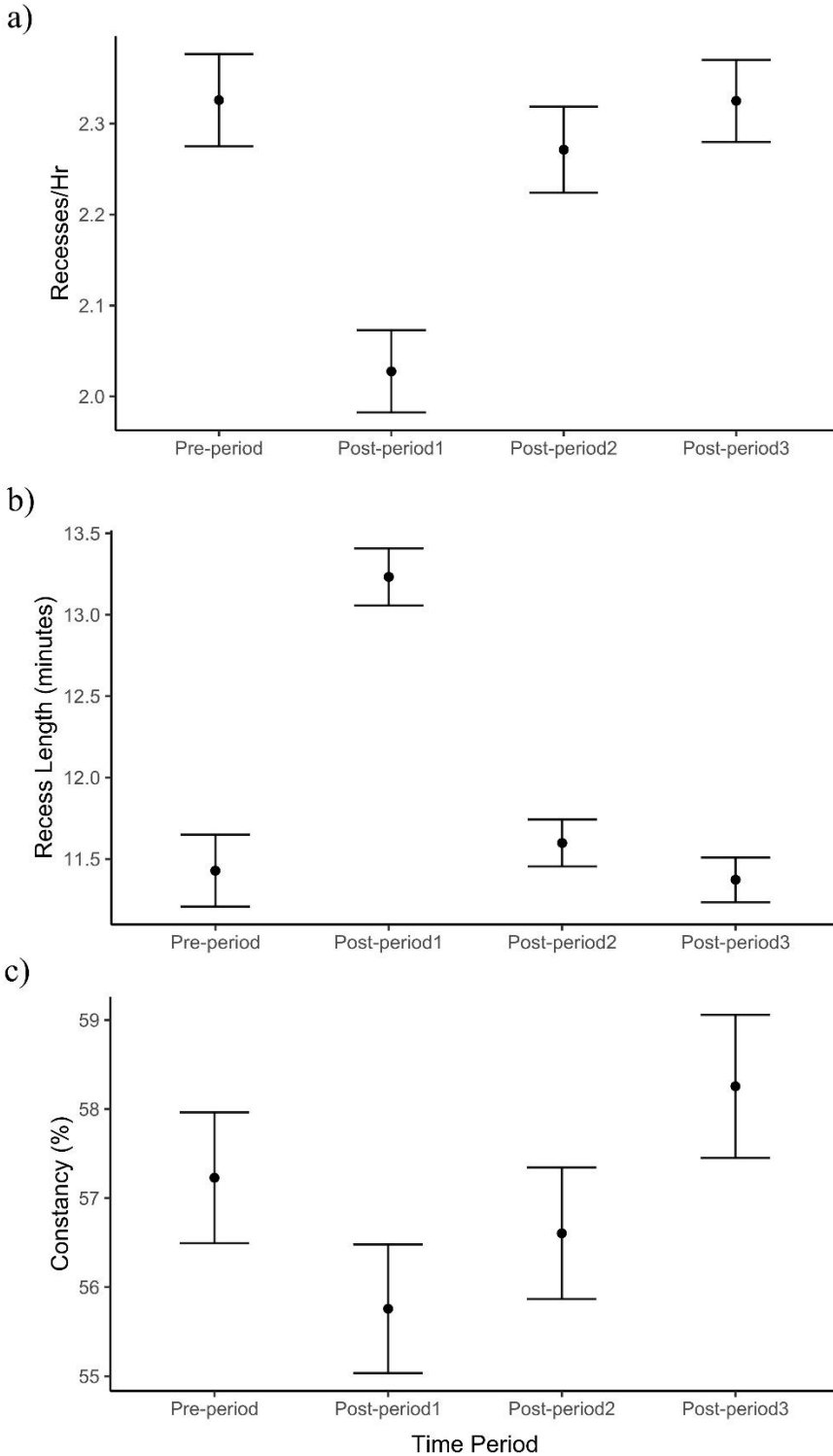


Figure 3.2. The incubation recess rate, recess length, and constancy of 42 Mountain Bluebirds within each of four time periods. The pre-trial (control) period was measured prior to presentation of the predator model. Period 1 is the day of predator exposure, and the subsequent periods are the two days following. Means are shown \pm SE.

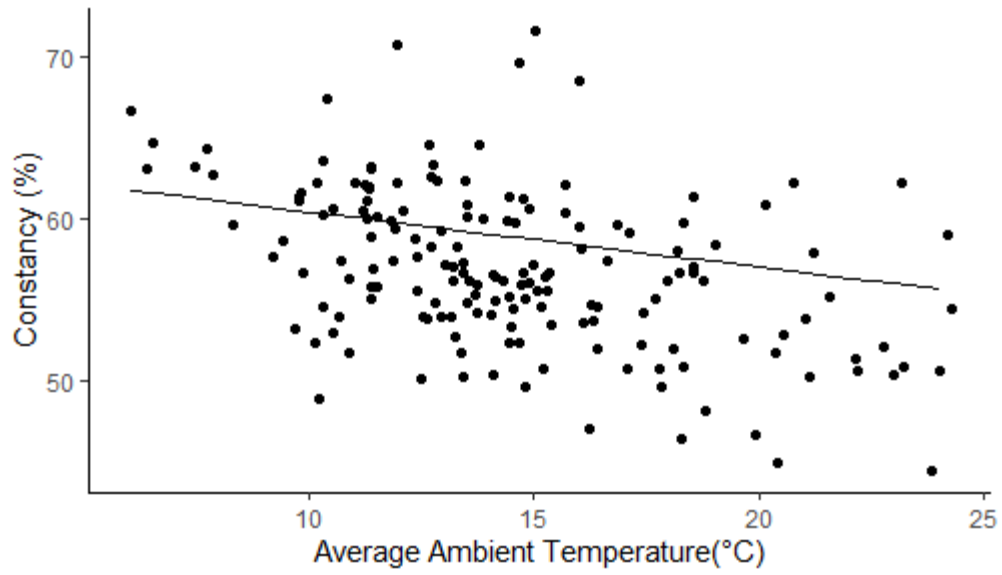


Figure 3.3. The relationship between female constancy of incubation in Mountain Bluebirds and average ambient temperature, controlling for aggression and period.

CHAPTER 4: GENERAL DISCUSSION

4.1 Overview

In this thesis, my primary objective was to investigate how the immediate threat of a nest predator influenced parental behaviour of Mountain Bluebirds (*Sialia currucoides*) and how individual variation in active defence behaviour and incubation rhythms was related to a range of independent variables.

In Chapter 2, I examined how the intensity of nest defence behaviour in Mountain Bluebirds may be influenced by a broad range of morphological characteristics (sex, age, colour intensity, body size, and body condition) and features of the nest (clutch size, laying date, breeding stage). In accordance with my predictions, the intensity of nest defence increased with clutch size and stage of breeding. In accordance with the reneating hypothesis, males defended more intensely than females in both the incubation and nestling stages of breeding likely because of a lower reneating potential (Power 1975). However, the parent's morphological characteristics were not shown to be related to nest defence intensity. These results indicate that the sex of the parent and reproductive value of the brood are the primary drivers of nest defence rather than body size or energy stores of the parents. This provides strong support for parental investment theory and the costs of reneating as potential determinant factors in nest defence intensity in Mountain Bluebirds.

In Chapter 3, I investigated how incubation rhythms (recess rate, recess length, constancy) of female Mountain Bluebirds changed when directly exposed to a model nest predator. I also examined how such changes were affected by morphological (age and body condition) and behavioural (aggression PCA score) characteristics of the female as well as the external ambient temperature and time period before and after exposure to a model predator. As

predicted, incubating females minimized activity (recess rate) around the nest following a perceived nest predation threat. This was likely done to reduce the attention of a nest predator now perceived to be in the area. Females seemed to compensate for the reduced number of trips to feed themselves by increasing the time spent away from the nest on each trip. However, these fluctuations in incubation rhythms were shown to persist for two days following exposure and returning to normal after that. These results seem to suggest that female Mountain Bluebirds place a high priority on regulating the temperature of the eggs even during the threat of nest predation. This is further supported by the fact that constancy during the three time periods after exposure to the model nest predator never significantly differed from the pre-trial. Incubation behaviour was not significantly affected by the ambient temperature before exposure to a nest predator. However, ambient temperature was shown to affect constancy after the predator trial, possibly because of a larger sample size.

4.2 Research Implications & Directions of Future Study

My study provides new insights into nest defence by Mountain Bluebirds and the potential trade-off between defending the current nest and renesting. My findings imply that the intensity of nest defence in Mountain Bluebirds is driven primarily by the perceived value of the offspring and the reproductive cost associated with not defending them. This may explain why males who appear to have a lower renesting potential than the females (Power 1975) were shown to contribute a greater defensive effort.

My finding that the incubation response of female Mountain Bluebirds to simulated predation risk only lasted two days suggests that females are under pressure to resume normal incubation rhythms as soon as possible. Previous research has primarily examined the effect of nest predation by repeated predator presentations throughout the incubation period. My study, on

the other hand, is one of the first to investigate the immediate affects of exposure to a perceived nest predator on incubation rhythms. My research suggests that the requirements of the developing embryos limit the degree of behavioural plasticity of incubating female Mountain Bluebirds toward the threat of nest predation.

This research provides evidence suggesting that the reproductive value of the offspring and the renesting potential of the parents are the primary drivers of nest defense intensity in breeding Mountain Bluebirds rather than any of the morphological characteristics of the parents. My study also demonstrates the potential trade-offs of stable incubation rhythms and limiting the risk of exposing the nest to predation. However, the reproductive consequences of the “climate of fear” presented by the risk of nest predation will require more study (Zanette et al. 2011, Ibáñez-Álamo et al. 2015), as they are vital to understanding the adaptive value of antipredator responses.

Nesting birds seem to have a threshold distance a potential nest predator crosses that triggers a defensive response (Montgomerie and Weatherhead 1988). Attacking a potential nest predator too early may reveal the location of the nest. Future research might use my study as a framework to examine the degree to which the distance of the perceived nest predator from the nest might influence the intensity of nest defence and what prompts a defensive response from the parents. A more comprehensive understanding of the underlying variation in the response to nest predation may be crucial in regions with human-induced habitat change (Martin 1993, Ibáñez-Álamo et al. 2015). Therefore, a comparison of nest defence intensity in different habitats or geographical locations may also be worth pursuing. Regarding incubation behaviour, there is limited information on how incubation rhythms might fluctuate after daylight hours when a significant proportion of nest predation attempts occur (Weidinger 2010, Ibáñez-Álamo et al.

2015). Exploring incubation behaviour during nighttime should be looked into for future studies in breeding passerines.

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