

A sex difference in the behavioural response of nesting mountain bluebirds (*Sialia currucoides*) to a mounted predator

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Abstract Passerine nests can benefit parental fitness, but defense against predators may be costly. Although this paradigm is well studied, no studies have been conducted on mountain bluebirds (*Sialia currucoides*). We observed the response of 17 bluebird pairs with nestlings to a mounted bobcat (*Lynx rufus*) and two controls. Bluebird pairs clearly differentiated the mounted predator and males moved closer to the bobcat than to the controls whereas females did not. This system is ideal to further refine nest-defense hypotheses.

Keywords Anti-predator · Behaviour · Bluebird · Nest defense · Passerine

Introduction

Nests containing young represent a significant potential fitness benefit for both the female and male of socially monogamous, biparental care, passerine species. In turn, for many passerine species, nest predation has been shown to be the most important variable affecting fitness (Ricklefs 1969). The costs and benefits of nest defense behaviour have consequently been subject to a great deal of study within an optimality framework (Montgomerie and Weatherhead 1988). The costs include a potentially increased risk of predation for the defending parent (Montgomerie and Weatherhead 1988), as well as a loss of time and energy, which could be directed towards other activities (Buitron 1983). The benefit is an increased survival

probability for the young (Knight and Temple 1986; O-lendorf and Robinson 2000) and consequently increased fitness for the defending parents.

A common approach to testing nest defense behaviour is to place a live or mounted predator near an active nest and observe the behaviour of the parents (e.g., Michl et al. 2000; Pavel 2006). We quantified the behaviour of females and males in mountain bluebird (*Sialia currucoides*) pairs in response to three disturbances at their nests during the nestling period. In one treatment, a human walked to and immediately away from the nest. In the other two treatments, in addition to approaching the nest, the human placed a mounted bobcat (*Lynx rufus*) or a cardboard box of similar dimensions to the bobcat at the base of the nest. The stimulus remained in place for 5 min. We predicted that bluebird parents would exhibit the strongest response to the bobcat and weaker responses to the human intrusion and the cardboard box. Such a result would suggest that bluebirds distinguish between a novel disturbance near their nest and the presence of a predator.

The intensity of nest defense behaviour has been used to test predictions from parental investment theory (e.g., Rytkonen 2002) since it reflects the degree of investment of each parent in the nest. Parental-investment theory predicts increased nest defense behaviour on the part of one sex or another in different systems (Montgomerie and Weatherhead 1988; McLean and Rhodes 1991) and numerous studies have shown such differences (e.g., Hogstad 2005) although others have not (e.g., Tryjanowski and Golawski 2004). We do not make an a priori prediction about, which sex will exhibit the greatest response. A greater response by one sex or the other will suggest which factors might be important in this system and can direct future studies. To our knowledge, nest defense has not been tested in any bluebird species (*Sialia* spp.) to date.

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Materials and methods

Study population and area

The mountain bluebird is an altricial, cavity-nesting, sexually dichromatic passerine with an average adult weight in our study population of 33.5 ± 2.8 g (mean \pm SD, $n = 44$). Clutches in Alberta, Canada are incubated for 12–15 days and young spend between 17 and 22 days in the nest before fledging (Pearman 2002). The study was conducted near Lethbridge, Alberta ($49^{\circ}41'39''\text{N}$, $112^{\circ}50'27''\text{W}$, 914 m altitude) in habitat consisting of open prairie rangeland, farmland and coulees along a river bank. There is a low density of residential housing and sparse stands of trees and low shrubs. The study was conducted on 17 banded but otherwise unmarked adult pairs tending nests containing a brood of one to seven young (mean = 4.6) aged nine to 17 days (mean = 12.8). Animals had previously been marked and banded by the Mountain Bluebird Trails Conservation Society, a not-for-profit organization that runs a bluebird box monitoring program. Boxes were visited every 3–7 days throughout the incubation and nestling phases as part of this same program (Pearman 2002). At the time of sampling 10 boxes contained first clutches, four had second clutches, and three were clutches of unknown order. Since mountain bluebird pairs co-operatively raise hatched young and defend the nest during the nestling period (Power 1966), we assumed that any adult in the vicinity of the nest was one of the pair tending the nest. All nests were in standard top-opening Alberta mountain bluebird nest boxes (Pearman 2002). Nest boxes were mounted at approximately 1.5 m from the ground on the fence posts of barbed wire cattle fences. All animals were treated in accordance with the principles and guidelines of the Canadian Council on Animal Care.

Trials

Trials took place between 20 June, and 1 August 2003 and were conducted on clear sunny days with warm temperatures (20–35°C). Preceding each trial the observer placed a ground-level blind 24 m from the bluebirds' nest box and placed four 1.5 m high bamboo posts at the cardinal points at a 12 m radius from the nest box. Preliminary observations revealed that a 12 m radius area allowed visual observations of the male and/or the female within the experimental area in most pairs. The observer then left the area for at least 1 h (120.6 ± 52.4 min, mean \pm SD). On his return; he unobtrusively took his place behind the blind with two covered props: (a) a taxidermy bobcat (*Lynx rufus*; $67 \times 40 \times 18$ cm) and (b) a brown cardboard box of similar size ($68 \times 27 \times 31$ cm). Bobcats are present in the area (Nowak 1999) and have been reported as predators of

passerines and cavity nesting birds (Semel et al. 1988; Delibes et al. 1997). The observer waited 15 min with his entire body out of sight and then waited until both adults were outside the 12 m radius perimeter (6.6 ± 15 min, mean \pm SD). He then presented the first of three treatments. The presentation order was random. The treatments were as follows the observer (a) walked to 0.5 m from the nest box, bent down, straightened and immediately returned to the blind, hereafter called the "human" treatment, (b) walked to 0.5 m from the nest box, placed the cardboard box on the ground and then returned to the blind, hereafter called the "box" treatment or (c) walked to 0.5 m from the nest box, placed the mounted bobcat on the ground and returned to the blind, hereafter called the "bobcat" treatment. Note that the "human" element remains a component of both the 'box' and 'bobcat' treatments. After returning to the blind, the observer waited until an adult entered within 12 m of the nest box to start recording behaviour.

Behaviour was recorded for the subsequent 5 min using a digital video camera (Canon NTSC 2P70 MC) in the blind. When both adults were within the 12 m radius area the observer filmed both if they were close enough together to maintain focus and sufficient detail. If they were not, the observer filmed the more active individual while verbally recording any activity of the less active individual into the video camera microphone. The observer also counted into the camera microphone each vocalization he heard while one or both birds were within 12 m of the nest box. It was not always possible to distinguish which bird was vocalizing, so vocalizations were recorded for the pair and not the individual.

Upon completion of 5 min of recording, the observer immediately removed the prop irrespective of the bluebirds' position (within or outside of the 12 m radius area). Following the 5 min of recording and removal of the prop, the observer waited a further 15 min behind the blind and then presented the second treatment. The same procedure was repeated for the third treatment. Upon completion of the final 5 min of recording, the trial was concluded.

From the video, the locations of the male and female of a pair were recorded every 5 s through each 5 min presentation. Location was classified as less than 12 m or greater than 12 m from the nest box. This yielded a maximum of 60 observations per bird per treatment and three treatments per bird per trial. A total count of the number of vocalizations made by the pair during each 5 min trial was also tabulated.

Statistical analyses

Main effects

Two response variables are used. "Proportional proximity" is the proportion of observations of the bird within 12 m of

the nest box out of the total number of observation intervals from the bird's first recorded interval within 12 m of the nest box. Since the male and female rarely arrived together generally one bird of each pair was observed for 60 intervals and the other for fewer. In one case a bird was observed for fewer than 15 intervals (75 s) from its first observation within 12 m of the nest box. This record did not constitute enough information to calculate a proportion and we treated it as missing data. 'Vocalization rate' was calculated as:

$$vr = \frac{v}{(ib \times 2) + im + if}$$

where vr is the vocalization rate, v is the number of vocalizations recorded during the 5 min treatment and ib , im , and if are, respectively, the number of intervals where both the male and female, only the male, and only the female were within 12 m of the nest. The denominator represents the number of intervals per bird available for vocalizations but the vocalization rate does not distinguish, which bird is vocalizing.

In all cases, non-parametric statistics are used because sample sizes prevent the data from meeting parametric assumptions. All significance levels are 0.05. Friedman tests are used to test for an effect of treatment on male proportional proximity, of treatment on female proportional proximity and of treatment on vocalization rate. Three Wilcoxon signed-rank tests are used to test for a difference in proportional proximity between sexes of a pair in the human, box and bobcat treatments, respectively.

Controlling for potential confounding variables

We considered several potential confounding variables. Although it was randomized, the order in, which treatments were presented could confound a treatment effect (see Knight and Temple 1986), or a sex effect if the effect of order applies to only one sex. We tested order against proportional proximity for males and females and against vocalization rate using Friedman tests. None were significant (proportional proximity for males, $n = 9$, $\chi^2 = 2.38$, $df = 2$, $P = 0.303$; proportional proximity for females, $n = 7$, $\chi^2 = 2.30$, $df = 2$, $P = 0.317$; vocalization rate, $n = 9$, $\chi^2 = 0.06$, $df = 2$, $P = 0.972$).

All but one (in the female treatment and sex effect tests) or two (in the male treatment and vocalization tests) nest boxes held a first clutch. With so little variation, it is unlikely that clutch is driving any observed effects. The Friedman and Wilcoxon signed-rank tests make comparisons between the same individual or pair across three treatments and between members of a pair, respectively. Consequently, the age of young and number of young do

not vary between treatments for a given individual or pair, or between individuals of a pair. Therefore, although there is variation in the age and number of young between pairs, this variation does not account for observed effects.

An effect of sex might result if one sex was more likely to arrive within the experimental area first (Hobson et al. 1988). This could result from the first bird behaving differently independent of sex, or from the first bird being observed for a longer period, which, if behaviours change with time during the observation interval, could result in an arrival order behaviour bias. Wilcoxon signed-rank tests of the proportional proximity of the bird that arrived first versus second in the human, box and bobcat treatments show no significant effects (human, $n = 5$, $Z = -1.48$, $P = 0.138$; box, $n = 8$, $Z = -0.42$, $P = 0.674$; bobcat, $n = 7$, $Z = -0.68$, $P = 0.498$). Such a confound might also apply to a treatment effect, however, there was very little variation in the number of observation intervals for the birds in treatment tests. For human, box and bobcat treatments for both the male ($n = 9$) and female ($n = 7$), the median and maximum values are 60 intervals. The minimum number of intervals are 43, 60, and 50 for male human, box and bobcat treatments, and 45, 31, and 47 for female human, box and bobcat treatments.

Results

The proportional proximity of bluebird males differed significantly with treatment ($n = 9$, Friedman $\chi^2 = 11.8$, $df = 2$, $P = 0.003$; mean ranks human = 1.2, box = 2.1, bobcat = 2.7). The mean ranks show that the proportional proximity for the bobcat treatment was the highest. The same effect is not evident in the females ($n = 7$, Friedman $\chi^2 = 0.96$, $df = 2$, $P = 0.618$; mean ranks human = 2.0, box = 1.7, bobcat = 2.2) although the response to the bobcat elicited the highest mean rank value. Median values are highest for the bobcat treatment in both males and females (Fig. 1). The vocalization rate per pair differed significantly between treatments ($n = 9$, Friedman $\chi^2 = 8.22$, $df = 2$, $P = 0.016$; mean ranks human = 1.7, box = 1.6, bobcat = 2.8) with the greatest mean rank in response to the bobcat.

When observations were compared between pair members, males had significantly higher proportional proximity values than females in face of the box and bobcat treatments but not in face of the human treatment (Table 1).

Discussion

When presented with an object next to the nest, most bluebirds in our study perched within sight of the nest and

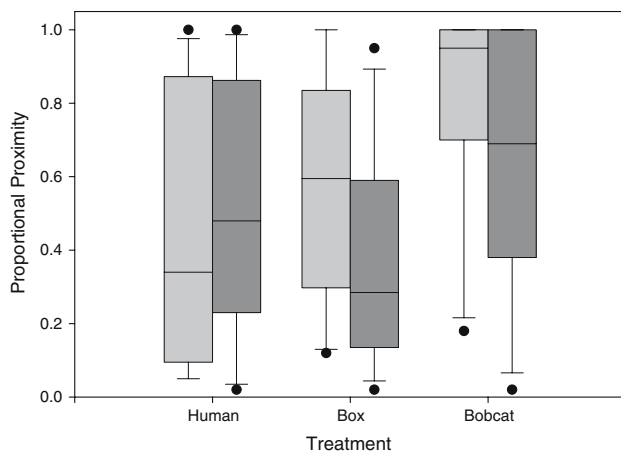


Fig. 1 The proportion of observations a bird spent within 12 m of the nest box during 5-min observation periods for males (*light grey boxes*) and females (*dark grey boxes*) in each of three treatments. Sample sizes are: male human (12), female human (10), male box (14), female box (13), male bobcat (12), and female bobcat (11). Box-plots indicate the 10th, 25th, median, 75th, and 90th percentiles. Dots indicate outliers

Table 1 The results of three Wilcoxon signed-rank tests for a sex difference in the proportional proximity values of bluebird pairs for a human, box and bobcat treatment at their nests

| Treatment | <i>n</i> | <i>Z</i> | <i>P</i> |
|-----------|----------|----------|----------|
| Human | 5 | -0.944 | 0.345 |
| Box | 9 | -2.073 | 0.038 |
| Bobcat | 7 | -2.032 | 0.042 |

vocalized, flying at intervals of less than a second to several minutes between different perches. Only infrequently were birds seen to swoop at the object. Some individuals were never observed within the experimental area while others quit the area on or soon after presentation of the treatment and did not return.

Our results suggest that nesting bluebird pairs, particularly males, distinguish between a novel object and a mounted predator and adjust their response accordingly. Male mountain bluebirds exhibited a different proportional proximity response to the three treatments with the highest response to bobcat treatment. This result is supported by the vocalization rate per bluebird pair, which also differed significantly between treatments and was highest for the bobcat treatment.

Curio (1975) has shown that pied flycatchers (*Ficedula hypoleuca*) show a similar nest defense intensity to mounted and live predators, supporting the use of mounted predators to test passerine anti-predator behaviour. Our results further support the use of mounted predators to examine this topic.

Our results also show that males and females of mountain bluebird pairs differ significantly in the proportion of observations they spend less than 12 m from a mounted predator next to their nest. Males have been observed to defend nests at a higher intensity than females during the nestling stage in other avian systems (e.g., Rytkonen et al. 1993). Using an optimality framework, Montgomerie and Weatherhead (1988) suggest a series of factors that could explain differential intensity in nest defense behaviour between sexes. These include confidence of parenthood, re-nesting potential, perception of risk, life history characteristics, the ability to raise young unaided, past parental effort and parental interactions in nest defense.

Our findings do not support Montgomerie and Weatherhead's (1988) prediction that the female's nest defense intensity should exceed that of the male in this species based on confidence in parenthood. Mountain bluebirds are similar to eastern bluebirds (*Sialia sialis*) where confidence in parenthood is lower for males than for females (Meek et al. 1994). Our results also do not support the prediction that the brighter bluebird male may be more vulnerable and should therefore be more cautious (Baker and Parker 1979). The results agree with the prediction that if one sex is unable to raise young alone, it should invest more in nest defense. Male mountain bluebirds are rarely observed raising chicks alone whereas females are (L. Sarsfield, personal communication).

The difference we observed in proportional proximity, however, does not necessarily reflect a difference in parental investment on the part of males and females. Anecdotally, in our study females vocalized longer, at a higher rate and from a greater distance than males. Males and females might therefore be using different strategies with comparable costs and efficiencies where the female strategy may include an attempt to avoid revealing the location of the nest (Zimmermann and Curio 1988).

The time lost to nest defense in mountain bluebirds may be more costly for females or negligible for both sexes. Garcia et al. (1993) found that food supplemented mountain bluebird females did not lose weight during the nestling phase whereas non-supplemented females did, suggesting that female mountain bluebirds may be food limited. Alternatively, the cost of time lost may be negligible for both sexes. In the ecologically similar western bluebird species (*Sialia mexicana*; Mock 1991) found that adults feeding nestlings were neither food limited nor working maximally.

However, the cost of distraction displays or a closer proximity to the predator on the part of the male may also be negligible. Although Curio and Regelman (1986) argue that mobbing behaviour can be very risky, the less aggressive strategy of male bluebirds (which were almost

never observed to dive towards the predator) may not be, particularly in face of a cryptic terrestrial predator, such as the bobcat, once it is identified. There is very little evidence for the costs of such tactics (see Montgomerie and Weatherhead 1988; Lima 1993). Although more has come to light with the advent of miniature video cameras to monitor nests (Pietz and Granfors 2005) a successful attack on the parent by the predator, once it is identified, may be very rare. There is also little information on the efficiency of alternative components of nest-defense behaviour, although there is correlational evidence that it can deter predators (Olendorf and Robinson 2000). Consequently, male and female bluebirds may both be incurring only a minimal cost for different nest defense strategies that have similar efficiencies.

Our study shows that mountain bluebird pairs respond more intensively to a mounted predator than a novel object near a nest containing young. Males defending nests are more proximate to the mounted predator than females, which may be risky. Based on these result, and given that thousands of mountain bluebird boxes are maintained in North America, combined with the ease of observation in relatively open terrain, we propose that this is a useful model system to further explore issues of nest defense.

References

- Baker RR, Parker GA (1979) Evolution of bird coloration. *Philos Trans R Soc Lond Ser B Biol Sci* 287:63–130
- Buitron D (1983) Variability in the responses of black-billed magpies to natural predators. *Behaviour* 87:209–236
- Curio E (1975) The functional organization of anti-predator behavior in the pied flycatcher: a study of avian visual perception. *Anim Behav* 23:1–115
- Curio E, Regelmann K (1986) Predator harassment implies a real deadly risk: as reply to Hennessy. *Ethology* 72:75–78
- Delibes M, Blazquez MC, Rodriguez-Estrella R, Zapata SC (1997) Seasonal food habits of bobcats (*Lynx rufus*) in subtropical Baja California Sur, Mexico. *Can J Zool* 75:478–483
- Garcia PFJ, Merkle MS, Barclay RMR (1993) Energy allocation to reproduction and maintenance in mountain bluebirds (*Sialia currucoides*): a food supplementation experiment. *Can J Zool* 71:2352–2357
- Hobson KA, Bouchart ML, Sealy SG (1988) Responses of naive yellow warblers to a novel nest predator. *Anim Behav* 36:1823–1830
- Hogstad O (2005) Sex-differences in nest defence in fieldfares *Turdus pilaris* in relation to their size and physical condition. *Ibis* 147:375–380
- Knight RL, Temple SA (1986) Why does intensity of avian nest defense increase during the nesting cycle. *Auk* 103:318–327
- Lima SL (1993) Ecological and evolutionary perspectives on escape from predatory attack: a survey of North American birds. *Wilson Bull* 105:1–47
- McLean IG, Rhodes G (1991) Enemy recognition and response in birds. *Curr Ornithol* 8:173–211
- Meek SB, Robertson RJ, Boag PT (1994) Extrapair paternity and intraspecific brood parasitism in eastern bluebirds revealed by DNA-fingerprinting. *Auk* 111:739–744
- Michl G, Torok J, Garamszegi LZ, Toth L (2000) Sex-dependent risk taking in the collared flycatcher, *Ficedula albicollis*, when exposed to a predator at the nestling stage. *Anim Behav* 59:623–628
- Mock PJ (1991) Daily allocation of time and energy of western bluebirds feeding nestlings. *Condor* 93:598–611
- Montgomerie RD, Weatherhead PJ (1988) Risks and rewards of nest defense by parent birds. *Q Rev Biol* 63:167–187
- Nowak RM (1999) Walker's Mammals of the world. The Johns Hopkins University Press, Baltimore
- Olendorf R, Robinson SK (2000) Effectiveness of nest defence in the Acadian flycatcher *Empidonax vireescens*. *Ibis* 142:365–371
- Pavel V (2006) When do altricial birds reach maximum of their brood defence intensity. *J Ethol* 24:175–179
- Pearman M (2002) Mountain bluebird trail monitoring guide. Red Deer River Naturalists, Red Deer
- Pietz PJ, Granfors DA (2005) Parental nest defense on videotape: more reality than 'myth'. *Auk* 122:701–705
- Power HW (1966) Biology of the mountain bluebird in Montana. *Condor* 68:351–371
- Ricklefs R (1969) An analysis of nesting mortality in birds. *Smith Contrib Zool* 9:1–148
- Rytkonen S (2002) Nest defence in great tits *Parus major*: support for parental investment theory. *Behav Ecol Sociobiol* 52:379–384
- Rytkonen S, Orell M, Koivula K (1993) Sex-role reversal in willow tit nest defense. *Behav Ecol Sociobiol* 33:275–282
- Semel B, Sherman PW, Byers SM (1988) Effects of brood parasitism and nest-box placement on wood duck breeding ecology. *Condor* 90:920–930
- Tryjanowski P, Golawski A (2004) Sex differences in nest defence by the red-backed shrike *Lanius collurio*: effects of offspring age, brood size, and stage of breeding season. *J Ethol* 22:13–16
- Zimmermann U, Curio E (1988) 2 Conflicting needs affecting predator mobbing by great tits, parus-major. *Anim Behav* 36:926–932