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RESEARCH ARTICLE

Interspecific competition for nests: Prior ownership trumps resource holding potential for Mountain Bluebird competing with Tree Swallow

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ABSTRACT

Interspecific competition over nest sites is common among cavity-nesting birds, but little is known about what determines the outcome of such contests, particularly whether or not prior ownership plays a role. Using a box removal and replacement experiment, I tested whether Mountain Bluebird (*Sialia currucoides*) or Tree Swallow (*Tachycineta bicolor*) had the higher resource holding potential (RHP). A different box-blocking experiment with paired boxes on territories measured the extent to which prior ownership influenced contest outcomes for both species. Behavioral observations in the pre-laying period showed more physical aggression by Mountain Bluebird against Tree Swallow. Nevertheless, Tree Swallow won 70% of boxes when neither species had prior ownership, suggesting Tree Swallow had a higher RHP. When their boxes were blocked, 24% of Tree Swallow usurped boxes from Mountain Bluebird, which did not differ statistically from the 33% of boxes usurped by bluebirds from swallows; thus, prior ownership does not guarantee winning the contest for either species. Currently, Mountain Bluebird arrives earlier in spring than does Tree Swallow and relies more extensively on prior ownership to retain nest sites. This advantage could be jeopardized if the migration schedule of Tree Swallow is accelerated due to climate change, and so it is important to understand the role of prior ownership in contests for nest sites for birds.

Keywords: interspecific competition, Mountain Bluebird, nest, resource holding potential, Tree Swallow

Competencia interespecífica por los nidos: la propiedad previa aumenta el potencial de explotación de recursos de *Sialia currucoides* frente a *Tachycineta bicolor*

RESUMEN

La competencia interespecífica por los sitios de anidación es común entre las aves que anidan en cavidades, pero poco se sabe sobre lo que determina el resultado de estas disputas, particularmente si la propiedad previa juega o no un rol decisivo. Usando un experimento de remoción y reemplazo de cajas, evalué si *Sialia currucoides* o *Tachycineta bicolor* presentaron el mayor potencial de explotación de recursos (RHP por sus siglas en inglés). Un experimento diferente de bloqueo de cajas realizado con cajas pareadas en los territorios estableció cómo la propiedad previa influenció el resultado de la competencia entre las dos especies. Las observaciones de comportamiento en el período anterior a la puesta mostraron una mayor agresión física por parte de *S. currucoides* hacia *T. bicolor*. A pesar de esto, *T. bicolor* ganó el 70% de las cajas cuando ninguna de las especies tenía la propiedad previa, sugiriendo que los individuos de *T. bicolor* tuvieron mayor RHP. Cuando sus cajas fueron bloqueadas, 24% de los individuos de *T. bicolor* usurparon cajas de *S. currucoides*, lo que no difirió estadísticamente del 33% de las cajas usurpadas por individuos de *S. currucoides* a *T. bicolor*. De este modo, la propiedad previa no garantiza ganar la disputa para ninguna de las especies. Actualmente, los individuos de *S. currucoides* llegan más temprano en la primavera que los individuos de *T. bicolor* y se sustentan en mayor grado de la propiedad previa para retener los sitios de anidación. Esta ventaja podría verse amenazada si el esquema de migración de *T. bicolor* se acelera debido al cambio climático, y por ende es importante entender el rol de la propiedad previa en las disputas por los sitios de anidación de las aves.

Palabras clave: competencia interespecífica, nido, potencial de explotación de recursos, *Sialia currucoides*, *Tachycineta bicolor*

INTRODUCTION

Many animals meet in pairwise competitions over resources such as food, mates, or breeding sites. The outcome of such competitions depends on a number of factors, including resource holding potential (RHP), which involves attributes such as large size, good body condition, or experience that give an individual greater fighting ability (Lozano 1994, Pryke and Andersson 2003). There may also be a "pay-off asymmetry" (Nijman and Heuts 2000) between the competitors, such that the individual who values the resource more has greater motivation to fight.

Irrespective of RHP, however, a prevalent pattern in animal contests is that the previous owner of the resource wins against intruders trying to usurp it (Kemp and Wiklund 2001, review in Kokko et al. 2006). This prior residence effect can be an evolutionarily stable determinant of contest outcomes settled by the principle "owner always wins" (Maynard Smith and Parker 1976), although scenarios in which owners are sometimes tested by intruders and may lose the resource seem more likely to evolve (Kokko et al. 2006).

In many field studies, it is difficult to disentangle why a particular individual won a contest. For example, RHP and ownership may be correlated if the strongest individuals are also those who tend to secure territories first (Leimar and Enquist 1984). In another scenario, ownership itself may increase physical advantages (Fayed et al. 2008) or increase knowledge about the resource (Bridge et al. 2000), which increases the motivation or ability of owners to fight. Distinguishing the separate roles of RHP and ownership on contest outcomes is needed to understand contest asymmetries and the evolution of such diverse behaviors as timing of spring migration in birds (Kokko 1999) and developmental rates in arthropods (Vollrath and Parker 1992).

A few studies have used experiments to tease apart the effects of RHP and ownership. For example, male jumping spiders (*Phidippus clarus*) that guard a female tend to win contests, but the outcome also depends partly on relative body size (RHP) of the intruder (Kasumovic et al. 2010). By contrast, prior ownership rather than RHP determines winter territoriality in the Eurasian Siskin (*Carduelis spinus*; Senar and Pascual 2015). Contest asymmetries have been studied mostly within species, but similar theory may apply to interspecific competition. Secondary cavity nesting birds may compete vigorously for a limited supply of tree holes to breed in (Newton 1994, Pearce et al. 2011, Charter et al. 2013). Often, 2 species differ so greatly in size or weaponry that the clear difference in RHP between them leads to predictable outcomes of competition for nest holes (Minot and Perrins 1986, Aitken and Martin 2008). For example, in North America, the aggressive European Starling (*Sturnus vulgaris*) may remove existing clutches of other cavity nesters to take over their nests, but the reverse does not occur (Ingold 1994, Koenig 2003, Wiebe 2003). If 2 species are more closely matched in RHP, however, contest outcomes may depend at least partially on prior ownership. The role of RHP vs. ownership has not been quantified for interspecific nest competition in such cases.

North American bluebirds (*Sialia* spp.) compete with Tree Swallow (*Tachycineta bicolor*) for nest holes (Gowaty 1981, Brawn 1990, Meek and Robertson 1994, Harris and Siefferman 2014). For the Mountain Bluebird (*S. currucoides*) in the West, there is debate about which species has greater RHP. Although bluebirds typically arrive on breeding sites earlier than do swallows, amateur naturalists often place nest boxes in pairs, ostensibly to protect the weaker bluebird from usurpation by the aggressive Tree Swallow (Prescott 1982). According to Power and Lombardo (1996), however, the Mountain Bluebird is more aggressive and also, by virtue of prior ownership, can defend any cavity they choose against the invading Tree Swallow.

Here, my goal was to measure RHP and effects of ownership in competitive interactions over nest boxes between Mountain Bluebird and Tree Swallow. I conducted 3 experiments: experiment 1 tested the flexibility of individuals to recognize and switch to alternate nest sites; experiment 2 forced competition between the species when the owners had prior ownership of their boxes; and experiment 3 was designed to determine the relative RHP of each species in the absence of a prior ownership advantage. I also conducted some observations to document which behaviors each species used to defend or usurp boxes and, in the case of Mountain Bluebird, which sex was more involved in nest defense.

METHODS

Study Site and Study Species

I studied birds nesting in boxes placed on fence posts in open grassland habitat in central British Columbia near Riske Creek (51°52′N, 122°21′W) and Williams Lake (51°7′N, 122°9′W) in 2014 and 2015. At the northern latitude and relatively high elevation of the study sites (915–1136 m a.s.l.), the difference in arrival and egg-laying between the species is probably less than at more southern and lower elevations. Here, the Mountain Bluebird appears after migration in spring about 2 weeks before the Tree Swallow, and the first egg dates in the population are on average 7 days before the Tree Swallow (personal observation), but there is overlap in nest initiation between species. Male Mountain Bluebird often arrive a few days before the females, and both sexes typically defend a box and also a feeding territory, which is at least 100 m from a neighboring bluebird (Power and Lombardo 1996). By comparison, Tree Swallow defend boxes but not feeding territories (Rendell and Robertson 1989). The Mountain Bluebird weighs ~30 g (Power and Lombardo 1996) and Tree Swallow ~20 g (Winkler et al. 2011).

At a location on a fence line, I placed a pair of identically constructed plywood boxes (16 × 16 × 30 cm with a 4 cm diameter entrance hole) on adjacent fence posts 6 m apart. All boxes used in the study were new, and no birds had previously bred at the sites on the fence lines. Hence, although individuals were unbanded, none would have had prior experience breeding in the boxes. I also tried to ensure a consistent and high motivation to fight for the

FIGURE 1. Experiment 3 set-up in open grassland habitat near Riske Creek, British Columbia. Two previously active nest boxes on adjacent fence poles owned by a Tree Swallow pair and a Mountain Bluebird pair were removed and placed on the ground, and a single, new, unowned box was erected on a new adjacent fence pole in the right foreground for the pairs to compete over.

box by separating box dyads by at least 400 m. This distance is larger than the size of a Mountain Bluebird territory, so that all individuals would suffer a cost of giving up their territory and moving to defend a new, unfamiliar area if they did not keep a box. No other natural cavities were available within the 400 m because the habitat was open grassland. By checking the boxes about every 2–3 days, I was able to track settlement of birds and appearance of nest materials.

Experiments

Experiment 1 was designed to control for potential effects of blocking and human disturbance on the willingness and ability of the focal pair to shift to an adjacent box in the absence of competition. I waited until either one Mountain Bluebird pair or one Tree Swallow pair settled at a dyad of paired boxes and had begun to construct a grass nest cup. I then blocked the entrance hole of that box with a piece of hard foam to test whether the pair shifted to the adjacent, empty box when it had no neighbors. This "control" experiment was only done in 2014.

Experiment 2, conducted in 2014 and 2015, involved dyads of boxes where both a Mountain Bluebird and Tree Swallow pair had settled and the females had begun to deposit nest material in adjacent boxes but before either had completed the nest cup or laid eggs. I flipped a coin at the first box dyad to determine whether the Mountain Bluebird's or Tree Swallow's box would be blocked and then alternated the species with the blocked box at subsequent dyads so that date did not differ between treatments. A piece of hard foam was inserted in the entrance of the blocked box and remained in place until one species laid eggs in the unblocked box, showing it had "won." In this experiment, each pair had the advantage of prior ownership of its box when trying to defend it from the other.

In experiment 3, conducted in 2015, I waited until a Mountain Bluebird pair and a Tree Swallow pair each began to deposit nest material in adjacent boxes as before, but this time removed both original boxes and replaced them with a single new box on a different fence pole 6–12 m from the original boxes (Figure 1). I alternated whether the new box was placed closer to the swallow's or bluebird's original site, and box placement did not affect the outcome ($\chi^2 = 0.16$, df = 1, $n = 30$, $P = 0.69$). In this scenario, neither pair had prior experience or ownership of the box and therefore was forced to compete without prior owner advantage for the nest.

Behavior at the boxes was easy to observe with binoculars from about 200 m. In 2014 and 2015, I recorded the frequency of aggressive behavior (chasing, attacking) and potential defensive behavior (blocking the nest hole, distance of perching from the box) at box dyads during 1–1.5 hour observation sessions occurring between 0930 and 1500 hr. A series of observations was conducted shortly after arrival (within 3–4 d) of a Tree Swallow pair to the site and prior to any treatments. A subset of the boxes was observed 24 hours after blocking to record the types of agonistic behaviors, but, because of time constraints, relatively few pairs could be observed. The purpose of behavioral observations was not to explain in detail variance in aggression between individuals, but rather to document the offensive or defensive behaviors involved in nest retentions or take-overs. Behaviors of Mountain Bluebird were kept separate by sex because each is easily distinguished by plumage from a distance (Power and Lombardo 1996), but data from Tree Swallow were pooled for the sexes because they are more difficult to distinguish from a distance.

Data Analysis

To not alter the willingness of birds to defend a box, I did not trap or mark them prior to the experiments, but the manipulations were conducted at different sites separated by at least 5 km in the 2 years, which is greater than the typical interyear dispersal distance of 1.1 km for Mountain Bluebird (Herlugson 1981) and 100 m for Tree Swallow (Winkler et al. 2011). It is therefore unlikely that any pairs were observed in both years. Tests were conducted using SPSS 20 (SPSS 2011) and with alpha set at 0.05 for 2-tailed tests.

RESULTS

Agonistic Encounters

At box dyads before the blocking experiments, physical contact between species was rare, occurring in 1 of 33

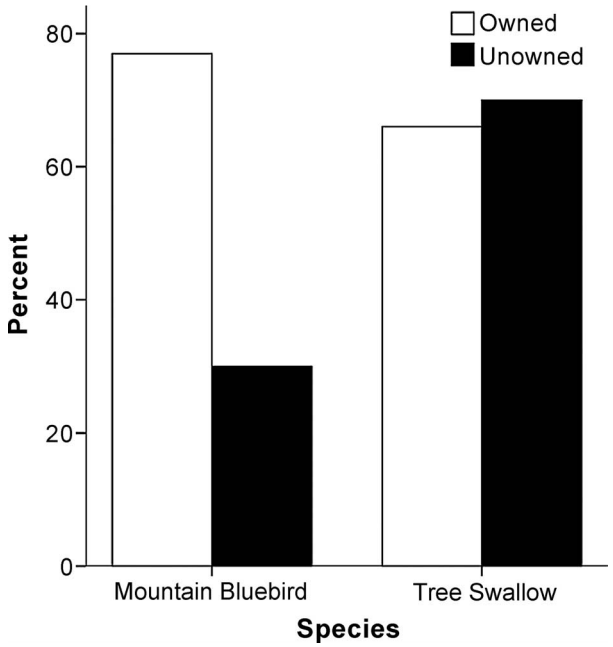

FIGURE 2. Percent of trials won by the species according to whether it was defending its previously owned box (experiment 2) or competing for a box previously unowned by either species (experiment 3). Sample size was 26 blocked Tree Swallow boxes and 24 blocked Mountain Bluebird boxes in experiment 2, and 30 contested boxes in experiment 3.

observation sessions at different dyads. In this instance, the male Mountain Bluebird grabbed the Tree Swallow in flight and both tumbled to the ground. More frequently, in 60% of the 33 sessions, a Mountain Bluebird chased and displaced Tree Swallows perched on the fence line near (1–10 m from) the Mountain Bluebird's box or chased Tree Swallow circling near (within ~3 m) the entrance to the bluebird's box. Both sexes of Mountain Bluebird chased Tree Swallow, but the male was involved more frequently (mean 3.56 attacks per hour) compared to his mate (1.98 attacks per hour; paired *t*-test; $t_{19} = 2.1$, $P = 0.05$). Directed aggressive behavior from a Tree Swallow toward a Mountain Bluebird was uncommon in this early period prior to box blocking; in 5 of the 33 sessions (15%), a swallow dive-bombed a bluebird perched at box dyads. However, Mountain Bluebird rarely (18% of observation sessions) approached the entrance hole of the Tree Swallow's box whereas the swallows more frequently (58% of 33 observation sessions) perched at the hole or tried to enter the bluebird's box, even though they had their own empty box available.

In most (10 of 11) observation sessions conducted after box blocking in experiment 2, both pair members of both species were still at the boxes 24 hours later. Sample sizes were small, but types of agonistic interactions were qualitatively similar to the pre-treatment situation. Mountain Bluebird with their own box blocked ($n = 5$) tried to enter the Tree Swallow box on average 5 times per hour, and swallows typically defended their box by sitting in the entrance hole and vocalizing. Mountain Bluebird did not try to dislodge Tree Swallow sitting in the entrance holes but did chase them when perched beside the boxes. Behavior of Tree Swallow with their own box blocked ($n = 5$) was qualitatively similar to the pre-treatment situation with swallows checking and trying to enter the bluebird's box on average 6.24 times per hour.

Experiments

In experiment 1, both species readily recognized and switched to a different box in the absence of competitors. All 7 Mountain Bluebird pairs and all 7 Tree Swallow pairs were depositing nest material in the adjacent empty box 24 hours after their original box was blocked. In experiment 2, 23% (6 of 26) Tree Swallow pairs with a blocked box usurped the one previously owned by Mountain Bluebird, whereas 33% (8 of 24) blocked bluebirds usurped the swallow's box. The frequency of usurpation did not differ between species ($\chi^2 = 0.65$, $P = 0.42$). When forced to compete for a new single box without prior ownership in experiment 3, Tree Swallow won the box in 21 of 30 (70%) trials, which was significantly greater than a 50-50 chance (binomial test, $P = 0.043$). When the 2 nest box competition experiments were compared (experiment 2 vs. 3), the probability of the Mountain Bluebird winning a competition for a nest site varied significantly according to whether it had prior ownership of the box; it won 77% of the time when it had prior ownership but only 30% when there was no prior ownership by either species ($\chi^2 = 7.2$, df $= 1$, $P = 0.007$). By contrast, prior ownership did not affect the Tree Swallow; its probability of winning was 66% with ownership and 70% in direct competition ($\chi^2 = 0.69$, df $= 1$, $P = 0.79$; Figure 2).

DISCUSSION

Competition between Mountain Bluebird and Tree Swallow for a nest box could be intense and the outcome was uncertain, with both species able to usurp boxes from the other owner in experiment 2, and both species able to win some, but not all, contests when fighting over a previously unowned resource in experiment 3. In this way, both seemed to follow the "partial respect for ownership" scenario discussed by Kokko et al. (2006) in which prior ownership is occasionally challenged and take-overs are possible. A few other experiments on interspecific nest competition in cavity-nesting birds have used reciprocal presentations of taxidermic models to quantify aggression (RHP) between 2 species (e.g., Král and Bicík 1992, Krist 2004, Pearce et al. 2011, Edworthy 2016), but to my

knowledge, none has measured the effect of prior ownership on the outcome.

Several classic studies on interspecific competition in other species of birds have noted the roles of RHP and arrival timing in obtaining a breeding territory on the landscape (e.g., between species of blackbirds: Orians and Willson 1964; gulls and shorebirds: Young 1976; warbler and flycatchers: Sherry and Holmes 1988). The focus of the current study, however, is qualitatively different from those studies because Mountain Bluebird and Tree Swallow were not competing for a general territory that included a range of resources such as food, shelter, and nesting areas, but only for a discrete resource (a particular nest site). In classic studies of interspecific territoriality, it is more difficult to interpret the "value" of the landscape for each competing species because their niches, and hence preference for resources, differ. By comparison, the value of the nest box in my experiments was likely similar for the Tree Swallow and Mountain Bluebird because both absolutely required a box to breed, and no alternate nests were nearby. In wild populations, the density and quality of artificial nests and natural cavities at a site may determine nesting alternatives (see Robles and Martin 2013) and the hence the willingness of individuals to fight for a certain site.

Forcing individuals to compete for a nest without prior ownership in experiment 3 showed that Tree Swallow had a higher average RHP than Mountain Bluebird, but this average difference in fighting ability between the species was not sufficient to predict the outcome of contests with certainty. The greater average RHP of Tree Swallow was intriguing because the larger Mountain Bluebird was actually more willing to make physical contact during aggressive encounters and made more directed chases toward the Tree Swallow. Instead of physical force, the Tree Swallow seemed to rely on a strategy of continued harassment and a steady presence near the box to gain access to the entrance hole, behavior that eventually wore down the defensive efforts of many Mountain Bluebird pairs. During observations, the Tree Swallow showed more intrusions, perching at the hole and/or entering the Mountain Bluebird's box more than vice versa. In the wild, the Tree Swallow may sometimes defend 2 cavities, presumably as alternate sites to breed if one nest fails (Winkler et al. 2011). The behavioral tactic of entering and occupying boxes is also common in intraspecific contests over nest sites among Tree Swallow (Stutchbury and Robertson 1987). Monopolizing the entrance hole may be effective for the Tree Swallow because I never observed Mountain Bluebird entering boxes to physically grapple with, and evict, swallows and only one incidence was seen in 10 years of fieldwork by colleagues working nearby (Jeannine Randall, personal communication). The higher RHP of the Tree Swallow is counter to the idea of Power and Lombardo (1996) that aggression by Mountain Bluebird gives them dominance and is sufficient for them to defend a nest against a single Tree Swallow pair.

Although the focus of the current study was not to explain variation in defensive behavior between individuals, some of the variation was clearly related to sex, with female Mountain Bluebird chasing Tree Swallow at 56% the frequency of males. Meek and Robertson (1994) also reported a male bias in Eastern Bluebird (*S. sialis*) chasing Tree Swallow but apparently more extreme, with females chasing at only about 4% the rate of males. Females may generally invest less in defense prior to laying because they face higher demands for foraging to accumulate nutrients for egg formation and so trade-off nest defense with foraging. Although Mountain Bluebird were not individually marked in this study, in the future it would be interesting to test whether philopatric (see Herlugson 1981) individuals value and defend their familiar nest box more than a newly colonizing pair.

As in many other species, individual "boldness" or aggression may be repeatable personality traits in Tree Swallow (Betini and Norris 2012) and in bluebirds (Duckworth 2006, Harris and Siefferman 2014). The random assignment of individuals to experimental groups should have controlled for personality types in my study, and although this was not the focus, at the individual level, there clearly may be selection for aggressiveness in environments with high competition for nest sites (Rosvall 2008). An alternate, but not mutually exclusive, explanation is that aggressiveness is learned based on past experience with rivals. For example, Northern Flickers (*Colaptes auratus*) learned to defend their cavity nests more strongly against European Starlings after being exposed to them (Wiebe 2004). Future studies could use experiments to examine the role of past experience vs. inherited personality type on the level of aggressiveness and vigilance of individual bluebirds.

Aggressive interactions and nest usurpations have been recorded among numerous other cavity nesting species (Rendell and Robertson 1991, Strubbe and Matthysen 2009). For example, Meek and Robertson (1994) noted that Tree Swallow usurped nests on 22% of 64 Eastern Bluebird territories, similar to the frequency in the current study, but because many of those territories contained multiple, clustered boxes, the risk of take-overs is difficult to compare directly. Similarly, 33% of Western Bluebird (*S. mexicana*) nests in Arizona were usurped by Tree Swallow, but there, flocks of 4–12 swallows often harassed a single bluebird (Brawn 1990). Harris and Siefferman (2014) found that 15% of Eastern Bluebird nests were lost to Tree Swallow that recently colonized the site in the Appalachian Mountains. In Europe, nest competition between 2 common species, the Great Tit (*Parus major*) and the Pied Flycatcher (*Ficedula hypoleuca*) is frequently

noted, but the greater difference in RHP between species makes the outcome of nest competition more predictable. The Great Tit can kill Pied Flycatcher in the nestbox (Merilä and Wiggins 1995), and tits successfully defended 97% of their previously owned boxes against the incomers (Slagsvold 1978) and 94% of their nests in the Netherlands (Samplonius and Both 2014).

Perhaps my most interesting finding was that prior ownership significantly increased the probability of winning for Mountain Bluebird but not for Tree Swallow. The average level of nest defense often changes with breeding stage in birds (Redmond et al. 2009), including bluebirds (Gowaty and Wagner 2010). In the experiments, the Mountain Bluebird often built up a slightly larger grass nest than the Tree Swallow because they were slightly more advanced, but the difference in energy investment in nest building between them would have been small. Theory suggests that parental defense should not be based on the amount of past breeding investment but rather future benefits (Curio 1987), and, in this respect, the species should have valued the resource nearly equally in both experiments because losing had the same cost (abandoning the area and moving to a new, distant location). Average nest defense levels may also depend on nest density and the number of competing floaters on the study site (Barber et al. 1996), but nest timing and number of competitors cannot explain the relative difference in performance of species between experiment 2 and 3 because such factors were the same for both treatments. Why the success of Mountain Bluebird increased significantly when they had prior ownership is not entirely clear. Knowledge of a particular box unlikely gave any physical advantage in fights that always occurred outside the box. Perhaps the Tree Swallow valued a box with foreign nesting material in it less than they valued a new box and so fought less intensively for it. When given a choice, the Tree Swallow preferred clean boxes to dirty boxes, presumably to avoid parasites (Rendell and Verbeek 1996), although they certainly can take over nest sites with existing nest material (Winkler et al. 2011).

Rather than, or in addition to, avoidance of parasites, the Tree Swallow may not fight as hard for preowned bluebird nests if their competitors may start laying soon. The Tree Swallow can destroy eggs of conspecific rivals (Winkler et al. 2011), but no destruction or usurpation of Mountain Bluebird nests occurred after bluebirds laid eggs during 3 years on my study area (personal observation), and, similarly, all swallow take-overs of bluebird boxes occurred prior to egg-laying in a study in Ontario (Meek and Robertson 1994) and in Arizona (Brawn 1990). Thus, if a nest with bluebird eggs is unusable for swallows, and if bluebird nest material is a cue that bluebirds could soon start to lay, swallows may be less willing to invest in a potentially long and costly fight for the site.

In cases of intraspecific competition, individuals arriving on the breeding site earliest are often the best quality and able to secure and defend the best locations by virtue of both higher RHP and priority ownership (Wiggins et al. 1994, Verboven and Visser 1998, Kokko 1999). With interspecific competition, if the species with the lower RHP arrives earlier, as seems to be the case with bluebirds and swallows, the early arriver's success at securing a nest will depend mainly on the strength of the prior ownership effect. Interspecific competition, however, is unlikely the only driver of earlier arrival dates of Mountain Bluebird compared to Tree Swallow in the northern part of their range. Rather, the Mountain Bluebird is simply able to take advantage of fruits and the relatively early phenological emergence of ground arthropod prey compared to the Tree Swallow, an aerial insectivore. Field experiments in other species have shown a positive association between phenological overlap in breeding activity and the frequency of interspecific aggression over nest sites (Slagsvold 1978, Gowaty 1981). Climate change thus has the potential to affect the outcome of interspecific nest competition by influencing the migration arrival timing of one or both species. Documented advancement of the timing of spring migration of Tree Swallow in response to climate change (Dunn and Winkler 1999) suggests that phenological overlap between swallows and bluebirds may be increasing and may reduce the competitiveness of bluebirds in the future. Hence, the role of prior ownership in determining the outcome of competition for nests or territories deserves further study in other populations and in other species, especially in light of changes in migration timing documented for many (Crick et al. 1997, Gordo 2007).

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