

Human-induced changes in the dynamics of species coexistence: an example with two sister species

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14.1 Introduction

Urbanization has eliminated habitat and resources of many avian species and this has had devastating consequences for their populations (Marzluff, 2001; Shochat et al., 2006). In response to this, humans have implemented conservation programmes, some of which have been extremely successful. For example, in many suburban areas as well as urban parks, the placement of nest boxes has led to species recovery and has promoted stable breeding populations (Griffith et al., 2008; Newton, 1994). However, these successes are not without consequences. By altering resource availability, humans can profoundly affect the evolution of adaptations for colonizing new habitat and can also alter the dynamics of species coexistence. At the same time, species that depend on man-made resources present a unique opportunity to gain insight into fundamental problems in ecology and evolution. By exercising fine control over the location, density and stability of these resources, we can use these systems to gain a detailed understanding of species replacement, evolution of colonization strategies, and rapid adaptation to human-altered landscapes. In this chapter, I will use long-term studies of the evolutionary ecology of western and mountain bluebirds as an empirical example to show how human alteration of the density and stability of nest cavities, through the placement of artificial nest boxes, has influenced these species' behaviour, population dynamics and ultimately, their coexistence.

14.2 Mechanisms of species coexistence

Identifying the mechanisms of species coexistence is one of the most difficult problems in ecology (Chesson, 2000). Trade-offs in performance are thought to underlie patterns of species coexistence (Baraloto et al., 2005; Kneitel & Chase, 2004; Tilman, 2004) as superior competitive ability often comes at the expense of dispersal ability, abiotic tolerances, reproductive investment or efficiency of resource use (Cadotte, 2007; Hughes et al., 2003; Pfennig & Pfennig, 2005; Tilman, 1994). Such trade-offs underlie niche differences between species which can allow for stable coexistence locally by increasing the strength of intraspecific competition relative to interspecific competition (Chesson, 2000).

In combination with trade-offs acting at a local scale, regional-scale processes also have the potential to strongly influence patterns of species coexistence (Amarasekare, 2003; Cadotte, 2007; Kneitel & Chase, 2004; Leibold et al., 2004; Tilman, 1994). For example, the competition–colonization trade-off, where species that are superior colonizers are inferior competitors (Amarasekare, 2003; Cadotte, 2007; Yu & Wilson, 2001), can impact regional diversity as species alternately colonize and become extinct from habitat patches over time. Colonizing species are often highly dispersive and arrive at new habitat patches first, but are then displaced from these patches once less dispersive, better competitors arrive. The long-term coexistence of such species depends on disturbance such that new habitat patches

must continually become available to enable the persistence of the colonizing species (Brawn et al., 2001; Levin & Paine, 1974). Thus, resource and habitat stability is an essential component underlying species coexistence.

In addition to competition–colonization trade-offs, regional patterns of diversity are also influenced by environmental heterogeneity. If resource availability or abiotic conditions vary across the landscape, species that dominate in one area may be at a disadvantage in another, ultimately fostering regional coexistence (Amarasekare & Nisbet, 2001; Kneitel & Chase, 2004; Snyder & Chesson, 2003). For example, if species vary in their ability to exploit resource-rich versus resource-poor habitat patches, this can alter competitive dominance across patches that vary in resource density (Palmer, 2003; Tessier & Woodruff, 2002). Thus, resource patchiness, stability and density are all key factors that influence patterns of species coexistence and urbanization can have both subtle and dramatic effects on all of these factors.

14.3 Urbanization and its impact on resource distribution and stability

In densely populated areas humans typically try to minimize the effects of natural disturbance. For example, in coastal areas humans erect bulkheads and other structures to stabilize a disturbance-prone beach habitat, in forest and grassland regions, fire suppression is used to protect local communities and forest and agricultural resources, and in major river corridors, levees, dams, and reservoirs are erected to control water levels to protect historically flood-prone areas from damage.

Such suppression of ecological disturbance means that habitat and resource stability have been fundamentally altered in many human-dominated ecosystems and this can have strong negative impacts on species adapted to disturbance-mediated habitats (Brawn et al., 2001). Interestingly, this frequently overlooked result of urbanization—habitat stabilization—is the opposite of the massive disturbance typically associated with urbanization. Yet, while it is true that urbanization causes major disturbance to many stable communities, it also simultaneously results in

stabilization of habitats that were previously disturbance prone as humans create a novel environment and then seek to protect and maintain it. How such habitat stabilization has influenced community composition and species adaptations for colonizing new habitat has been a largely overlooked question in the context of urban ecology research.

Secondary cavity nesting birds provide a clear example of species whose resource distribution, density and stability have been fundamentally altered by human intervention. The initial impacts of urbanization on these species are usually negative—factors such as deforestation, fire suppression, and the introduction of non-native cavity nesting species, typically decrease the availability of their most limiting resource—nest cavities—by reducing the number of dead trees where natural nesting holes are usually found or by adding novel competitors to the environment (e.g. Prescott, 1982). On the other hand, in more recent years, many secondary cavity nesting species have become the focus of conservation efforts and this has resulted in widespread implementation of nest-box programmes to provide an abundance of nesting sites for these highly charismatic species. Across the world, nest boxes have been used to maintain healthy populations [e.g. bluebirds, *Sialia* spp. (Gowaty & Plissner, 1998; Guinan et al., 2000) and wood ducks, *Aix sponsa*, in North America (Semel & Sherman, 1995)] and to rescue threatened populations [e.g. Eurasian rollers, *Coracias garrulus*, in Spain (Rodriguez et al., 2011); Gouldian finch, *Erythrura gouldiae*, in western Australia (Brazill-Boast et al., 2012)] of secondary cavity nesters. Even beyond formal conservation efforts, in many areas, the placement of nest boxes is common among the general public, not just in rural areas, but also in urban parks and suburbs as a way of attracting favoured avian species. In all of these cases, nest boxes are placed to maximize breeding densities of a particular species and not to mimic natural resource distributions and dynamics.

The distribution and persistence of natural tree cavities varies depending on habitat characteristics, climate and the source of cavity creation [e.g. by cavity excavators such as woodpeckers versus fungal or insect damage (Cockle et al., 2011)]. In North America, new habitat for cavity nesters is often created as a result of forest fire, which produces

an abundance of dead snags and is quickly colonized by primary excavators that make new cavities which pave the way for colonization of secondary cavity nesters. The density of nest cavities in these burned forests can be quite high, but their distribution is often clumped and any particular nest cavity may last only for a few years (Chambers & Mast, 2005; Lehmkuhl et al., 2003). Nest boxes, on the other hand, are usually distributed evenly across the landscape and will last for as long as humans actively clean, replace and repair them. Moreover, nest-box trails are usually placed near human settlements and roadways while naturally occurring habitat occurs most frequently in rural or wilderness areas. Consequently, the placement of nest boxes is likely to drastically alter the density, stability and distribution of a key resource that is known to be limited and to impact both intra- and interspecific competition in birds (Newton, 1994).

In the next section, I describe how manipulation of this resource has produced insights into competitive dynamics of two sister species, western and mountain bluebirds (*Sialia mexicana* and *S. currucoides*, respectively) and how human conservation programmes in response to urbanization may be altering the coexistence and evolutionary trajectory of many secondary cavity nesting bird species. I then discuss more generally how the effects of urbanization on resource stability may be an overlooked but potentially important factor in understanding the diversity of species in urban environments.

14.4 Empirical example: disruption of bluebird colonization cycles

14.4.1 Historical context for species coexistence and evolution of dispersal strategies

Before the widespread placement of nest boxes, new bluebird habitat was largely created by forest fire which generates suitable habitat by opening up understory vegetation and creating dead snags. Eventually, as the forest regrows, bluebirds are no longer able to breed in these habitat patches because snag density decreases and regrowth of the forest eliminates the open meadows bluebirds depend on to forage for insect prey (Guinan et al., 2000;

Power & Lombardo, 1996). Recent studies on the distribution, density and stability of nest cavities in post-fire forests of North America indicate that nest cavities occur in densities of 10–20 per hectare, are usually clumped in their distribution, and can last for up to 25 years (Lehmkuhl et al., 2003; Remm & Löhmus, 2011; Saab et al., 2002). Most cavities, however, have a much shorter longevity with a median life span of 14 years (Cockle, Martin & Wesolowski, 2011). Thus, historically, bluebirds' habitat and main limiting resource—nest cavities—were patchily distributed and relatively ephemeral.

The successional nature of post-fire habitat meant that the persistence of bluebirds depended on their ability to continually recolonize new habitat patches (Schieck & Song, 2006). In general, the two species have evolved distinct strategies for finding and settling in new habitat. Mountain bluebirds are more dispersive than western bluebirds (Guinan et al., 2000; Power & Lombardo, 1996) and are frequently among the earliest colonizers following forest fires (Hutto, 1995; Schieck & Song, 2006), whereas, western bluebirds often show delayed patterns of colonization (Kotliar et al., 2007; Saab et al., 2007). However, once new habitat is found, competition for nest cavities among these and other secondary cavity nesting species is intense and often involves aggressive displacement (Brawn & Balda, 1988; Duckworth, 2006b). Western bluebirds, while less dispersive and slower to find new habitat, are on average, more aggressive than mountain bluebirds and rapidly displace them when they colonize newly available habitat (Duckworth & Badyaev, 2007). Thus, the coexistence of these two species is at least partly explained by regional scale processes in the form of a competition–colonization trade-off where mountain bluebirds are the superior colonizers because of their higher dispersiveness and western bluebirds are the superior competitors due to their higher aggressiveness.

The apparent trade-off between aggression and dispersal seen at the species level in this system is not upheld at the intraspecific level as western bluebirds have evolved two distinct dispersal strategies in which there is a positive association between dispersal and aggression. Highly aggressive western bluebird males tend to leave their natal populations and disperse to new areas to breed, whereas,

non-aggressive males tend to remain in their natal population and eventually acquire a territory near relatives (Duckworth & Badyaev, 2007; Duckworth, 2008). Aggression and dispersal are functionally integrated in western bluebirds because colonization of new habitat patches by dispersing males requires the ability to outcompete earlier arriving heterospecific competitors for nesting sites and territories. Yet, aggression is costly as it trades off with parental care (Duckworth, 2006b) and once the earliest arriving western bluebirds have secured territories, there is strong selection for lower levels of aggression. Concordant with this strong selection, aggression rapidly shifts over time such that within 5–10 years of colonization, populations display much lower levels of aggression (Duckworth, 2008). This shift is adaptive because nonaggressive males are poor competitors and benefit from remaining in their natal population where they can gain a territory by cooperating with relatives. These males have higher fitness than aggressive males in older, well established populations but rarely, if ever, are observed colonizing new populations, whereas, aggressive males have the highest fitness when dispersing to new populations where density of conspecifics is low (Duckworth, 2008).

Distinct dispersal strategies such as those observed in western bluebirds are common in species that depend on ephemeral or successional habitat, especially when habitat patches are moderately stable (such as post-fire habitat) allowing the persistence of multiple generations, and thus a benefit to a philopatric strategy, before the patch disappears (Crespi & Taylor, 1990; Harrison, 1980; Johnson & Gaines, 1990; Roff, 1994). Thus, the historical distribution and stability of natural nest cavities likely played an important role in the evolution of western bluebird's distinct dispersal strategies. Moreover, the differences between mountain and western bluebirds in dispersal and competitive behaviour were also likely shaped and maintained by the natural distribution of this crucial resource. Recent human-induced changes in the distribution and stability of nest cavities are changing these dynamics. In the next section, I explain how nest-box programmes are impacting the dynamics of colonization and possibly the coexistence of these species.

14.4.2 Human placement of nest boxes: impacts on behaviour and species coexistence

In the late 1930s changes in logging and agricultural practices severely limited the availability of snags with nest cavities and western bluebirds' were extirpated from many parts of the northwestern United States where they were once common, particularly at the easternmost limit of their northern range edge (Duckworth & Badyaev, 2007). While mountain bluebird populations were also affected by this cavity limitation, their broader elevational range and more highly dispersive nature meant that they were able to maintain populations throughout this area. The widespread implementation of nest-box programmes, starting in the late 1960s, led to population increases for both species in the lower elevation valleys (Duckworth, 2006c). When nest boxes were first placed throughout the valleys of Montana, the site of our studies, mountain bluebirds reached these areas first. Yet, as western bluebirds expanded their range and moved back into these areas, they rapidly displaced mountain bluebirds, with complete species replacement occurring in less than 10 years in several populations, which have been closely monitored for over 30 years (Duckworth & Badyaev, 2007). Thus, the initial processes of colonization of this newly created man-made habitat mimicked the colonization patterns observed in natural post-fire populations. However, nest-box populations differ in several important ways from post-fire habitat and there is evidence that these differences are influencing the dynamics of colonization.

In Montana, nest boxes are usually placed in a linear transect and are spaced evenly (usually 100–200 m apart) along roadways. The goal of nest-box programmes is to try to maximize the number of breeding pairs and therefore, to place boxes at a minimum distance of adjacent bluebird territories. This distribution differs substantially from post-fire habitat in which nest cavities are often clumped and unevenly spaced (Saab et al., 2002). Thus, in contrast to a common criticism of the use of nest boxes—that people are increasing the density of available nest cavities beyond natural densities—the end result of such 'nest-box trails' is the creation of a much less patchy habitat with a more evenly distributed resource.

Such a distribution of nest cavities can influence habitat selection, settlement patterns, and ultimately the behavioural phenotype of the population. Bluebirds prefer territories with multiple cavities (Plissner & Gowaty, 1995; Saab et al., 2002), and in western bluebirds, the most aggressive males are most likely to obtain such preferred territories. Moreover, western bluebirds appear to use nest cavity availability as a primary factor in habitat choice over and above other habitat characteristics (Duckworth, 2006a). Using this information, we compared settlement patterns of males in a study site where nest cavity density varied naturally to a site where nest boxes were evenly distributed. In the naturally varying population, we observed that the distribution of nest cavities across the landscape influenced settlement patterns and created areas of high and low aggressiveness that corresponded to areas with many versus few nest cavities. In particular, at this site, there was a higher density of nest cavities in open compared to more forested habitat resulting in an overrepresentation of aggressive males there (Duckworth, 2006a). Such an assortment of aggressive types in relation to variation in nest cavity density is not possible in nest-box populations where nest boxes are distributed evenly across the landscape. Thus, local intraspecific competitive dynamics differ substantially between natural versus nest-box populations as variance in territory quality (at least in relation to the number of nest cavities) is much greater in natural compared to man-made habitat. This leads to hotspots and coldspots of competition in natural populations, whereas in man-made habitat, intraspecific competition is likely more spatially consistent.

The distribution of nest boxes is also likely to have important impacts on interspecific competition. In both bluebird species, more aggressive males acquire larger territories compared to less aggressive males; however, in mountain bluebirds, the relationship depends on whether they have a conspecific or heterospecific neighbour ($F_{1,20} = 4.43$, $P < 0.05$; Figure 14.1A). Specifically, territory size and aggression were only linked in mountain bluebirds when their nearest neighbour was another mountain bluebird ($F_{1,12} = 6.68$, $P = 0.02$, $b_{ST} = 0.60$), whereas, there was no relationship between territorial spacing and aggression when their nearest neighbour was

a western bluebird ($F_{1,6} = 0.01$, $P = 0.91$, $b_{ST} = 0.05$, Figure 14.1A). In western bluebirds, more aggressive males acquired larger territories ($F_{1,61} = 7.22$, $P < 0.01$; Figure 14.1B) and territories with more nest cavities ($F_{1,61} = 4.43$, $P < 0.05$; Figure 14.1B) and this relationship was not influenced by the identity of their nearest neighbour (interactions between species identity of nearest neighbour and aggression on territory size: $F_{1,95} = 0.17$, $P = 0.68$).

Mountain bluebirds are larger than western bluebirds and so require larger territories (Figure 14.1C; see also Pinkowski, 1979). However, we found that, in the presence of western bluebirds, mountain bluebirds' territories were significantly smaller than if their neighbour was another mountain bluebird ($t = 2.26$, $P = 0.03$; Figure 14.1D). The territory size of western bluebirds did not depend on which species was their nearest neighbour ($t = 0.84$, $P = 0.40$; Figure 14.1D). These results suggest that western bluebirds are able to displace mountain bluebirds during the process of colonization by crowding them out. Western bluebirds' higher aggression gives them the upper hand in boundary disputes and this causes the territories of any neighbouring mountain bluebirds to be smaller than would otherwise occur. These results also have implications for the link between nest cavity density and coexistence of the two species. If the distance between adjacent nest cavities is greater than the optimal territory size of mountain bluebirds, this can limit the ability of western bluebirds to crowd them out of an area because they will not breed close enough to mountain bluebirds to encroach on their territory. However, if nest cavity density is high, territory boundaries will be primarily determined by competitive interactions between the species.

To test this idea, we surveyed populations in which the density of nest boxes significantly differed and found that the two species were more likely to coexist when boxes were placed at a lower density (nested ANOVA: $F_{3,107} = 7.73$, $P < 0.001$; Figure 14.2). The correlation between nest cavity density and coexistence suggests that these species may differ in their ability to exploit resource-poor versus resource-rich habitat—a common trade-off mediating local coexistence (Palmer, 2003; Tessier & Woodruff, 2002). Mountain bluebirds may be limited in resource rich areas by the presence and

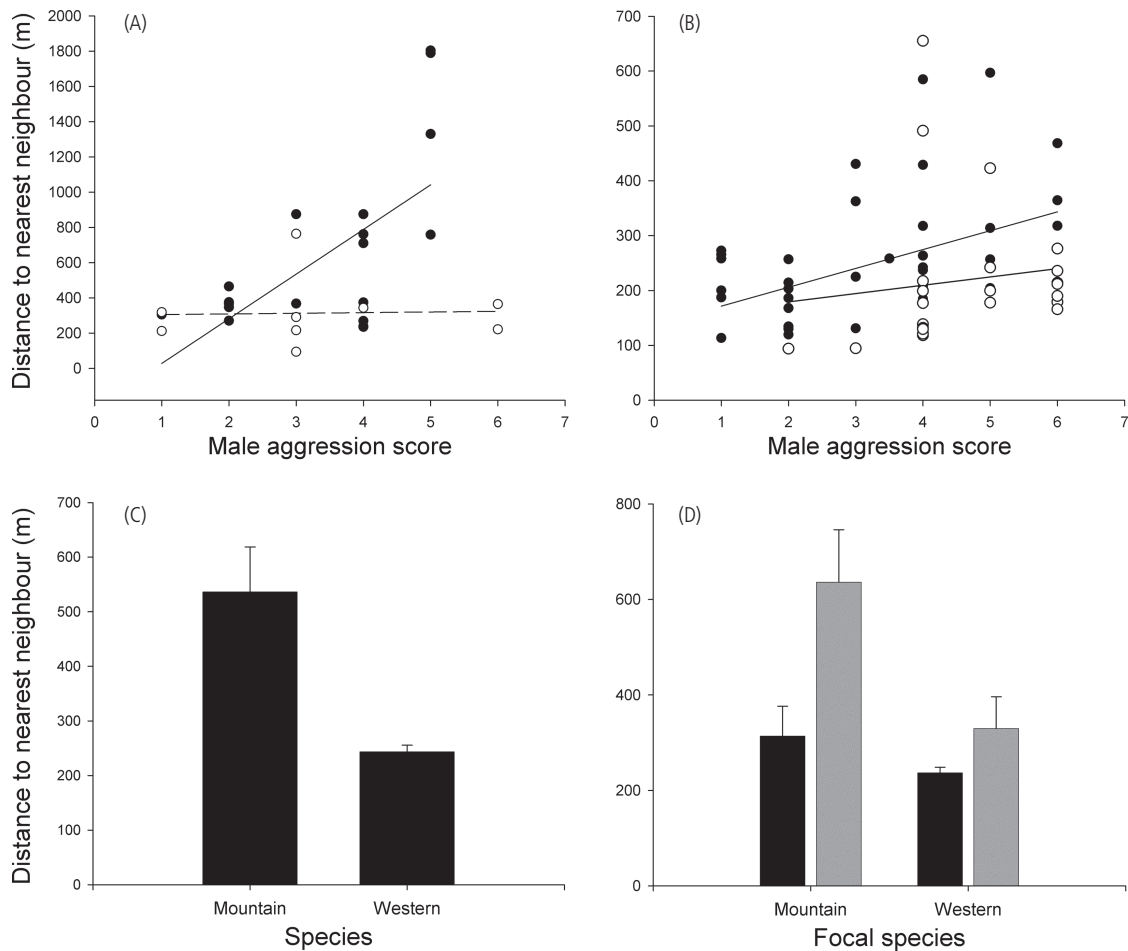


Figure 14.1 Relationship between distance to nearest neighbour and aggression for (A) mountain and (B) western bluebirds. In (A) open circles indicate territories in which the neighbour was a western bluebird and closed circles indicate territories in which the neighbour was a mountain bluebird. In (B) open circles indicate multi-box territories and closed circles indicate single-box territories. (C) Mountain bluebirds maintained greater distances from their nearest neighbour than western bluebirds. (D) This distance was significantly smaller if their nearest neighbour was a western bluebird (black bars). Spacing of western bluebirds did not depend on whether their neighbour was a western (black bars) or mountain (grey bars) bluebird. Bars indicate mean \pm standard error and numbers on bars are sample sizes.

higher competitive ability of western bluebirds. On the other hand, western bluebirds may be limited in resource-poor areas if breeding at high density is necessary for them to benefit from cooperative interactions with family groups. These results also have important implications for how nest-box populations may be changing the dynamics of species coexistence. Because the distribution of nest cavities in post-fire habitat is patchy and uneven, some nest cavities are clumped and some are relatively

isolated in their distribution. Thus, there may be more opportunities for the two species to coexist in these natural habitat patches compared to nest-box populations simply because there is more variability in the distances between nest cavities in post-fire populations.

Another major consequence of nest-box placement is that humans are replacing an ephemeral resource with a highly stable resource. In the context of a competition-colonization trade-off, the creation

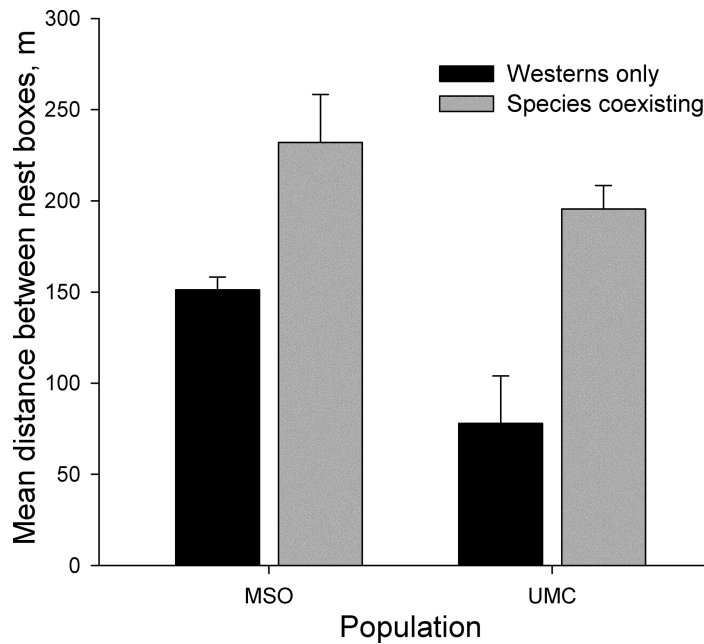


Figure 14.2 Coexistence of western and mountain bluebirds is significantly more likely when nest boxes were placed at a low compared to high density. Shown are data from four nest box populations that were all created at approximately the same time (15–20 years ago). Nest box trails were paired within valleys (MSO and UMC) to control for site-specific habitat variation.

of stable habitat is always disadvantageous to the better colonizer and advantageous to the better competitor (Levin & Paine, 1974). Thus, for bluebirds we would expect that, in areas of suitable habitat for both species (in this case lower elevation valleys), western bluebirds would permanently replace mountain bluebirds. As discussed above, this is exactly what we have observed in low-elevation nest-box populations in Montana (Duckworth & Badyaev, 2007). Many of these sites were first colonized by western bluebirds in the late 1970s and early 1980s and nest-box trails have been continuously maintained in these areas since that time. Western bluebirds' displacement of mountain bluebirds appears to be permanent as these areas continue to show stable western bluebird populations into the present day. Any mountain bluebird territories that do occur are usually on the periphery of these populations in areas where they are likely to share only one territory boundary with western bluebirds and thus are less likely to be crowded out (R.A.D. personal observations).

Similar to the interspecific patterns observed, at the intraspecific level, the replacement of an ephemeral resource with a stable resource should also lead to the permanent replacement of a colonizing morph

within a species. In concordance with this prediction, we found that, in the oldest nest-box populations, the more aggressive and dispersive phenotype in western bluebirds was replaced with the nonaggressive, less dispersive individuals (Duckworth & Badyaev, 2007; Duckworth, 2008). Humans have diligently maintained nest boxes at these sites for many decades, up to 45 years in the earliest established population. In contrast, post-fire habitat is only suitable for bluebirds for up to approximately 25 years (Schieck & Song, 2006). Many of the nest-box populations that we monitor in Montana have already exceeded this longevity. Moreover, although a natural nest cavity can last for more than 20 years, most natural cavities persist for only a few years, yet, in many nest-box populations, the man-made cavities are never moved and damaged boxes are replaced with new ones. This means that, not only is habitat longevity lengthened in nest-box populations, but longevity of nest cavities is also substantially increased. This excessive cavity stability in nest-box populations should be a further boon to the nonaggressive philopatric morph of western bluebird which relies on nepotistic territorial inheritance (Duckworth, 2008). In post-fire habitat, opportunities for territorial inheritance are likely to occur less

consistently as snag density changes dynamically across a habitat patch during forest succession.

In conclusion, post-fire habitat on which bluebirds historically depended in the northwestern United States differs substantially from nest-box trails on which these species are becoming increasingly dependent. There is clear evidence that this novel man-made habitat is impacting coexistence of the two bluebird species and the evolution of behavioural strategies in western bluebirds. However, the long-term consequences of such habitat replacement are less clear. Specifically, there does not seem to be any danger of western bluebirds dominating mountain bluebirds in all areas of their range. Nest boxes are mostly concentrated in the lower elevation valleys and are often clustered around human population centres. Moreover, western bluebirds rarely breed above 2000 m in the northwest while mountain bluebirds can breed at elevations up to 3500 m (Guinan et al., 2000; Power & Lombardo, 1996). Finally, since the mid-1980s, climate warming is increasing the frequency of wildfire in the western United States (Westerling et al., 2006). This, in combination with recent changes in fire suppression policy, which allows more wildland fires to burn without suppression efforts, means that natural post-fire habitat is on the rise. All of these factors should increase opportunities for coexistence of the two bluebird species and also maintain behavioural variation within western bluebirds. However, an interesting potential side effect of increasing abundance of both natural and man-made habitats is the possibility for significant behavioural and ecological divergence between post-fire and nest-box populations of these species. This is a particularly intriguing possibility given that dispersal dynamics are likely to differ substantially between these habitats (Citta & Lindberg, 2007).

14.5 Concluding remarks

The bluebird example offers several important lessons for research on nest-box populations of other species. One seemingly ubiquitous characteristic of secondary cavity nesting species is that nest cavities are their main limiting resource and competition over them is fierce (Newton, 1994). This has led to unique strategies both within and among species

for acquiring this resource. For example, just in the populations that we monitor, species differ substantially in their strategies for obtaining this resource. In addition to mountain bluebirds' dispersiveness and western bluebirds' aggressiveness, the small house wren (*Troglodytes aedon*) fills a cavity with sticks reducing the hole size until no other species can fit inside, and tree swallows (*Tachycineta bicolor*) breed later than the other secondary cavity nesters maintaining a constant vigilance in order to take over a cavity as soon as the previous owner's nest fails or fledges. Such diversity of strategies suggests that competition for nest cavities is a major driver of behavioural evolution as has previously been shown for life history evolution of these species (Martin, 1992).

The use of man-made nest boxes is likely to change in some way the density, distribution, and stability of this crucial resource and as a consequence will alter the dynamics of species interactions and quite possibly evolution of behavioural and life history traits. Thus, if we are interested in understanding the behavioural and life history evolution of secondary cavity nesting species, then it is useful and probably necessary to try to place findings from nest-box populations into the context of natural populations. Knowledge of the historical habitat and resource distribution in which these species evolved—whether that is woodpecker excavated cavities in post-fire forests typical of North America, non-excavated cavities in an old growth tropical rain forest typical of South America, or non-excavated hollows in multi-century old eucalypts typical of Australia where there are no primary excavators—is crucial to understanding population dynamics and species interactions of this widespread group of birds.

More generally, I hope that this chapter brings attention to one of the more overlooked consequences of urbanization—the stabilization of habitat. This has relevance to current issues in urban ecology in two ways. First, stabilization of disturbance-prone habitat in the landscape surrounding urban centres will generally favour less dispersive species over colonizing species and may also influence the evolution of species dispersal strategies and species coexistence patterns. For example, recent studies of structures that stabilize coastal and stream

areas show that such man-made structures can significantly impact species composition and local diversity (Bulleri & Chapman, 2010; Suddeth & Meyer, 2006). Whether these effects are mediated directly through habitat stabilization or are due to other consequences of human-altered habitat is an open question. Second, the urban environment itself is highly stable and does not undergo periods of disturbance and succession that occur in many natural systems. Such lack of heterogeneity in environmental conditions that organisms experience within urban environments through space and time may provide a key to understanding an outstanding question in urban ecology: why biodiversity in such environments is so low even though population densities are high (Shochat et al., 2010). Identifying and comparing key features of the historical habitat and resource distribution and stability of urban species may offer important insights into why these species, in particular, are able to thrive in such a novel environment.

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