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Research article

Nest-site competition between invasive and native cavity nesting birds and its implication for conservation

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A B S T R A C T

Nesting cavities are often a limited resource that multiple species use. There is an ongoing discussion on whether invasive cavity nesting birds restrict the availability of this key limited resource. While the answer to this question has important conservation implications, little experimental work has been done to examine it. Here, we aimed to experimentally test whether alien cavity nesting birds affect the occupancy of cavities and the resulting breeding success of native cavity breeders in a large urban park located in Tel Aviv, Israel. Over three breeding seasons, we manipulated the entry size of nest boxes and compared the occupancy and breeding success of birds in nest boxes of two treatments. These included nest boxes with large-entrance and small-entrance holes. The large-entrance holes allowed access for both the native and invasive birds (the two main aliens in the park are the common mynas and rose-ringed parakeets). The smaller-entrance boxes, on the other hand, allowed only the smaller sized native cavity breeders (great tits and house sparrows) to enter the boxes but prevented the alien species from entering. We found that the large-entrance nest boxes were occupied by five different bird species, comprising three natives (great tit, house sparrow, Scops owl) and two invasive species (common myna, rose-ringed parakeet) while the small-entrance boxes were only occupied by the two native species. The alien common mynas and rose-ringed parakeets occupied 77.5% of the large-entrance nest boxes whereas native species, mainly great tits, occupied less than 9% of the large-entrance boxes and 36.5% of the small-entrance boxes. When examining the occupancy of those cavities that were not occupied by the aliens, natives occupied both the small and large-entrance nest boxes equally. Three quarters (78%) of the great tits breeding in the large-entrance boxes were usurped by common mynas during the breeding season and as a result breeding success was significantly lower for great tits breeding in the large-entrance boxes compared with the small-entrance boxes. The results of this study suggests that the invasive alien species can reduce the breeding potential of native cavity breeders both by exploiting the limited breeding resource (nest cavities) and by directly usurping cavities already occupied by the native species. Since the majority of large-entrance nest boxes were occupied by the larger alien birds, less native species bred in the limited number of unoccupied large-entrance nest boxes because of exploitation competition. We propose that for management purposes, nest-box programs that alter the entrance size of available natural cavities may be a practical approach, reducing the competition between native cavity breeders and alien invasive birds, and especially benefiting the smaller native cavity breeders.

1. Introduction

Human-caused invasion of alien species has been suggested as one of the major factors leading to the rapid decline in native biodiversity (Dybas, 2004; McKinney and Lockwood, 1999). Alien species have wide-ranging economic, social health-related

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(Pimentel et al., 2000) and ecological impacts (Lockwood and McKinney, 2002; Mack et al., 2000; Mooney and Hobbs, 2000; Simberloff, 2004; Shirley and Kark, 2009; Pimentel, 2011), and can transfer disease to humans as well as to domesticated and wild animals and plants (Altizer et al., 2003). After an alien species establishes itself, the damage to native biodiversity and to humans can be both difficult and expensive to mitigate. It is thus crucial to study alien species and to find practical ways to prevent, control, or at least retard, ongoing invasions using creative approaches that are both cost-effective and simple for managers to implement.

Alien invasive birds can negatively affect native species by a range of factors, such as predation (Elton, 1958; Moulton and Pimm, 1983; Simberloff and Boecklen, 1991; Duncan and Blackburn, 2004; Gurevitch and Padilla, 2004) and competition over resources. One of these factors is interspecific competition, which plays a major role in shaping ecological communities (Connell, 1983; Schoener, 1983; Roughgarden, 1983; Schluter, 2000; Dayan and Simberloff, 2005). Interspecific competition is mainly split into exploitation competition and interference competition (Case and Gilpin, 1974). Exploitation competition occurs indirectly through the use of a limited resource, which then becomes unavailable for other individuals (Minot and Perrins, 1986). Interference competition occurs when individuals prevent access to a limited resource through direct negative interactions such as aggressive acts (Wiens, 1989). Nest sites are one of the main limiting factors of population size for various secondary cavity breeding birds across a range of systems (Newton, 1994; Dhondt, 2011), and such sites are also used by many alien species.

Most studies dealing with nest-site competition between alien and native secondary cavity breeders have been observational (Pell and Tidemann, 1997; Harper et al., 2005; Hernández-Brito et al., 2014) rather than experimental (Strubbe and Matthysen, 2009). One of the limitations of observational studies seeking to study competition is that the less dominant species may be excluded and may therefore be missed entirely in the study, although they are central to testing exclusion by aliens. Experimental studies therefore have extra value in understanding the dynamics of the resource use. For example, Strubbe and Matthysen (2009) found a case of exploitation competition by experimentally blocking cavities used by the alien rose-necked parakeets in Belgium the previous year. The parakeets then switched to cavities previously occupied by the smaller native species, the nuthatches (*Sitta europaea*), thereby reducing the number of breeding attempts of the natives.

Two of the most successful alien birds globally, the common (Indian) myna (*Acridotheres tristis*; hereafter myna) and rose-necked parakeets (*Psittacula krameri*) are both cavity nesters. The common myna has been listed as one of the 100 worst (highest impact) alien invasive species globally by IUCN (Lowe et al., 2000). Mynas are very opportunistic birds when it comes to eating different types of food (Sol et al., 2012) and are known to cause damage to agriculture in their native India (Kale et al., 2012) and in several invaded areas. It has been suggested that the myna and ring-necked parakeets presence can lead to a decline in the breeding of native species (Feare and Craig, 1999; Blanvillain et al., 2003; Strubbe and Matthysen, 2007; Grarock et al., 2013a), because they breed in a variety of nest sites (Orchan et al., 2013) and in particular have been found to use nest cavities at high percentages (Pell and Tidemann, 1997; Harper et al., 2005; Orchan, 2007; Strubbe and Matthysen, 2009; Orchan et al., 2013). It is still unclear how much invasive species affect the occupation and breeding of other species (e.g., Strubbe and Matthysen, 2009; Grarock et al., 2013a).

The myna was first introduced into Israel in 1997 in the Yarkon Park in Tel Aviv (Holzapfel et al., 2006; Yom-Tov et al., 2012), and has an average weight of 91.6 ± 17.9 g Israel Bird Ringing Center). The rose-ringed parakeet (weight: 137.5 ± 23.3 g, Israel Bird Ringing Center) has been reported in the wild in Israel since as early as 1960 (Dvir, 1988), but expanded its range only in the 1980s (Shwartz et al., 2009). The house sparrow (*Passer domesticus*, average weight in Israel 29.7 ± 2.2 g; Kobi Meryom unpublished data) and great tit (*Parus major*, average weight 16.1 ± 1.1 g; Charter unpublished data) are the two most common native secondary cavity breeders in the Mediterranean ecosystem of Israel (Yavin, 1987; Charter et al., 2010; Yom-Tov et al., 2012) and both are significantly smaller than the two introduced species.

Nest predation of house sparrows and great tit nests in Israel by the two most common nest predators (black rats; *Rattus rattus* and Asian racer; *Coluber nummifer*) are rare (Charter, M., unpub. data). Since both predators are able to enter the smallest entrance nest cavities used for breeding birds, nest predation was probably not a major factor in shaping the evolution of nest site selection in Israel. In comparison, nest site competition between native species, both the inability of native cavity nesting species to breed due to lack of available nest sites (exploitation competition) (Charter et al., 2013; Goldshtein, 2013) and nest failure due to usurpation by larger native nest site competitors (interference competition) has been documented in Israel in areas without alien species (Charter et al., 2010a, Charter et al., 2013).

The two most common native cavity nesting species (house sparrow and great tit) are significantly smaller than the most common alien species (myna and rose-ringed parakeet). We therefore hypothesize that breeding of the native species may be limited due to the lack of nest sites resulting from both exploitation competition (cavities occupied by the alien species cannot be used by native species) and interference competition (alien species supplanting native species in the cavities). In this study, we aimed to experimentally examine the effect of cavity nesting alien bird species on the occupation of cavities and breeding success of native species, as well as to provide management recommendations for mitigating the impact of alien birds on native cavity breeders in the region.

We compared the occupancy of native birds in small vs. large-entry boxes. The alien birds in this system can only enter the larger entry boxes. We predicted that the number of native species breeding and the breeding success of the native birds would be higher in nest cavities that restrict the alien species from entering, thereby reducing nest site competition. Differences in the number of native breeding pairs in different nest boxes of different entry sizes may be due to a preference for a specific nest box entrance size (i.e. prefer one size entrance over the other) or to difference of availability of unoccupied nest boxes of a certain entrance size. Thus, our goal in this study was to use an experimental approach to examine to examine whether invasive cavity nesting birds affect the breeding potential and success of native cavity breeders and to better understand their implications for conservation.

2. Methods

The study took place in the Yarkon Park in Tel Aviv (32°02′N, 34°47′E), Israel's largest urban park, located in the northern area of the city along the Yarkon River and habitat to many alien avian species in Israel (Shwartz et al., 2009; Orchan et al., 2013). We placed nest boxes (20 cm W × 28 cm L × 36 cm H, wall thickness 17 mm) at 40–50 m intervals on eucalyptus trees (*Eucalyptus sp*., the most common tree in the park) at a height of 3–4 m, using a ladder during October 2010. Similar-sized nest boxes were used to those that had been successfully used by native species (house sparrow, great tit, hoopoe *Upupa epops* and Scops owls *Otus scops*) in the area in Israel (Charter et al., 2008; M. Charter unpublished data). All nest boxes had an internal entrance size of 60 mm, while the external entrance holes could be adjusted to a size of either 60 mm (large entrance) or 39 mm (small entrance) using a small metal restrictor plate (Dhondt, 2011) glued to the front of each nest box. The nest entrance sizes of the nest boxes were selected according to the preference of entrance sizes used by great tits breeding in natural tree cavities (35 mm–59 mm, mean 46 ± 9 mm; reviewed in Lambrechts et al., 2010). The internal height of nest boxes from the bottom of the nest was similar in all cases. The large-entrance nest boxes were similar to the natural native Syrian woodpecker (*Dendrocopos syriacus*) holes (the primary cavity excavator of the site), which can be accessed by both alien species and also two large common native cavity breeders species (hoopoe and Scops owls; Charter et al., 2008; Charter et al., 2010b). Small-entrance nest boxes (39 mm entrance) were placed that prevented the larger alien species and the two larger native cavity breeders (hoopoe and Scops owls) access to the nest but allowed the two most common native cavity breeders, the smaller native great tits and house sparrows, to enter (Charter et al., 2010a). A metal restrictor plate (Dhondt, 2011) was used for the small entrance plate to prevent the nest entrance from being enlarged by Syrian woodpeckers (Charter et al., 2010) and rose-ringed parakeets (Orchan et al., 2013). The two types of nest boxes were placed throughout the park at random one after each other to control for differences in habitat types during the 2011 (n = 39 large-entrance nest boxes; 36 small-entrance nest boxes), 2012 (n = 39 large-entrance nest boxes; 35 small-entrance nest boxes), and 2013 (n = 37 large-entrance nest boxes; n = 36 small-entrance nest boxes) breeding seasons (from February-mid July during 2012–2013).

We monitored all nest boxes once a week by climbing up to the boxes and checking the box directly by lifting the lid. We did this during each of the 2011–2013 breeding seasons (three breeding seasons in total), starting from the third week of February to mid-July, which coincides with the natural breeding season of the species at this site (Orchan et al., 2013). All breeding attempts, defined as nest boxes that were occupied by a species that built nests, were recorded. The occupiers of all nests were identified, including those abandoned in the earliest stage of building, as a particular species by examining the variety of nest building materials which are unique to each bird. Since the smaller native species cannot breed in nest boxes already occupied by the larger alien species the occupation of nest boxes was compared twice: we considered all the nest boxes and added only those nest boxes that were available, not occupied by other species. In an earlier work in the same study area during the 2004–2005 breeding seasons we found that the occupation of nest boxes was similar to the occupation of natural cavities (Orchan, 2007; Orchan et al., 2013). Nesting failure was also recorded in our data.

All statistical tests were two-tailed and the data was not distributed normally. We therefore used Chi-square and Fisher's Exact Test to compare the number of small vs. large cavity entrance nest boxes occupied in the 2011 to 2013 breeding season, to compare the number of species breeding in the two types of nest boxes, and to compare the number of tits that bred successfully in the two nest entrance types. Mann-Whitney *U* test was used to compare the number of young fledged between small and large entrance nest boxes in the 2011 and 2013 breeding seasons (no pairs bred in 2012). Statistical analyses were performed using SPSS for Windows version 20.

3. Results

3.1. Nest box occupancy

Overall, we found that the large entrance boxes were occupied during the three breeding season by five different bird species, comprising three natives (great tit, house sparrow, and Scops owl) and two aliens (common myna, and rose-ringed parakeet) (Table 1). In comparison, the small-entrance boxes were only occupied by the two native species (great tit and house sparrow, Table 1). Common mynas occupied the majority (62–74%) of the large-entrance nest boxes, followed by rose-ringed parakeets (occupying 5–14% of the boxes), great tits, Scops owl, and black rats (*Rattus rattus*), while great tits occupied most of the small-entrance nest boxes (19–37%), followed by house sparrows, black rats, and honey bees (*Apis mellifera*) (Table 1).

During the three-year study, alien species (common mynas and rose-ringed parakeets) occupied only the large-entrance nest boxes (77.5% of the nest boxes, SE = 5.5%, n = 3 years), while native species occupied only 8.7% (SE = 4.6%, n = 3 years) of the large-entrance boxes and 36.5% of the small-entrance boxes (SE = 1.9, n = 3 years). Overall only 9, 6 and 7 of the large entrance nest boxes remained unoccupied in 2011, 2012 and 2013, respectively. The difference between the number of nest boxes of each type (large- and small-entrance boxes) occupied by native species (great tits and house sparrows, Fig. 1a) vs. aliens (common mynas and rose-ringed parakeets, Fig. 2) was highly significant in all years (2011: $\chi^2 = 25.0$, $df = 1$, $P < 0.0001$, 2012: $\chi^2 = 47.0$, $df = 1$, $P < 0.0001$, and 2013: $\chi^2 = 30.44$, $df = 1$, $P < 0.0001$).

Native species (the number of species was pooled) bred in both small and large entry boxes, and significantly more in small-entrance than in large-entrance boxes during all three breeding seasons (Fig. 1a). When examining the nest box occupancy of those cavities that were available and were not occupied by the aliens, the native species occupied both the small and large-entrance nest boxes equally (Fig. 1b).

Specifically, great tits occupied more small-entrance nest boxes in 2011 ($\chi^2 = 4.3$, df = 1, $P < 0.05$) and 2012 ($\chi^2 = 15.1$, df = 1, $P < 0.001$) breeding seasons but not in 2013 ($\chi^2 = 0.52$, df = 1, $P = 0.69$). When considering only available nest boxes (nest boxes not occupied by other species), great tits bred in the small and large-entrance nest boxes equally during the 2011 (Fisher's Exact Test $p = 0.73$), 2012 (Fisher's Exact Test $p = 0.08$), and 2013 breeding seasons (Fisher's Exact Test $p = 0.69$).

3.2. Breeding success

In comparison to great tits that bred in the large entrance nest boxes, great tits breeding in the small entrance nest box fledged more young during both the 2011 (large entrance = 1.6 ± 0.98 nestlings, N = 5 vs. small entrance = 3.6 ± 0.6, N = 13; Mann-Whitney *U* test, $Z = -2.10$, $P < 0.05$) and 2013 (large entrance = 0.00 ± 0.0 nestlings, N = 4 vs. small entrance = 3.3 ± 1.2, N = 7; Mann-Whitney *U* test $Z = -2.08$, $P < 0.05$) breeding seasons. No great tits breeding attempts were recorded in the six unoccupied larger entrance nest boxes in 2012. The difference in the number of great tit fledgling between the different sized entrance nest boxes was because more great tits failed to fledge any young in the large-entrance nest boxes than in the small-entrance in 2013 but not 2011 (Fig. 3). The majority (7 of the total 9) of great tit breeding attempts that failed to raise young (all in the large-entrance nest boxes) failed due to active eviction by mynas, which built nests on top of the great tits' nests during incubation of the latter's eggs (3/9 nests) or after the eggs had hatched (4/9 nests).

In all the above cases the myna started adding nesting materials between our visits (one week) and in all boxes we found abandoned great tit eggs and remains of the dead tit nestlings underneath the myna nests. After a myna occupied a nest box, we found no great tits pairs breeding in the same nest boxes both during the same breeding season and in the following years. Mynas also occupied the two large entrance nest boxes that great tit pairs succeeded to fledge later in the 2011 breeding season, 2012 breeding season and 2013 breeding season. In addition to great tits,

Table 1
The mean percentage of nest boxes with large and small entrance sizes occupied by cavity breeding bird species in the Yarkon Park, Tel Aviv during the 2011, 2012, and 2013 breeding seasons. Number of nest boxes in parentheses ().

	2011		2012		2013	
	L (39)	S (36)	L (39)	S (35)	L (37)	S (36)
Native birds						
Great tit (*Parus major*)	12.82%[a]	36.11%	0.00%	37.14%	10.81%[a]	19.44%
House sparrow (*Passer domesticus*)	2.56%	0.00%	0.00%	2.86%	0.00%	2.86%
Scops owl (*Otus scops*)	2.56%	0.00%	0.00%	0.00%	0.00%	0.00%
Alien birds						
Common myna (*Acridotheres tristis*)	61.54%	0.00%	74.36%	0.00%	67.57%	0.00%
Rose-ringed parakeet (*Psittacula krameri*)	5.13%	0.00%	10.26%	0.00%	13.51%	0.00%
Other						
Black rat (*Rattus rattus*)	0.00%	0.00%	0.00%	2.86%	0.00%	2.78%
Honey bee (*Apis mellifera*)	0.00%	0.00%	0.00%	2.86%	0.00%	5.56%

[a] Three of the 5 great tits pairs in 2011 and all 4 great tits pairs in 2013 bred in the large entrance nest boxes were later supplanted by myna.

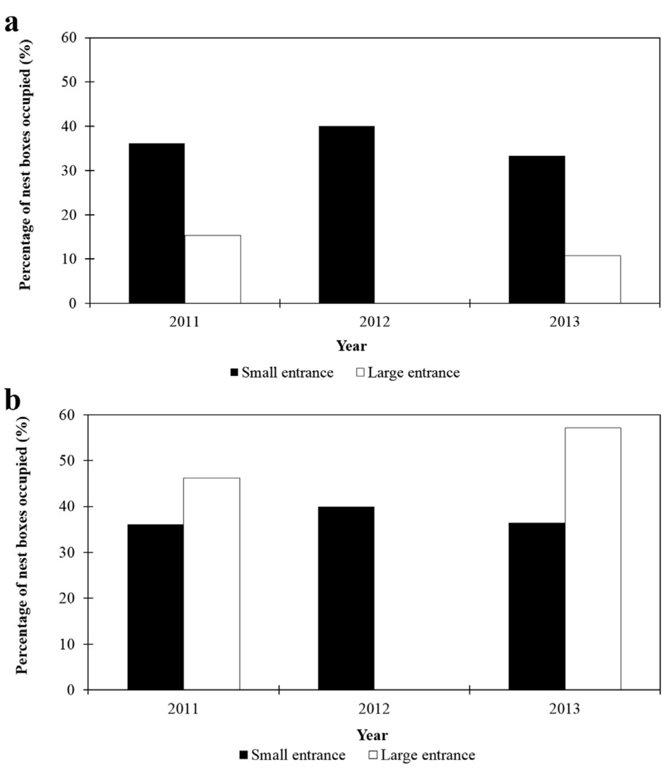

Fig. 1. a. The proportion of nest boxes occupied by cavity nesting birds during in the small and large entrance nest boxes by native species (great tits and house sparrows) during the 2011 ($\chi^2 = 4.25$, $df = 1$, $P < 0.05$), 2012 ($\chi^2 = 16.72$, $df = 1$, $P < 0.0001$), and 2013 ($\chi^2 = 4.17$, $df = 1$, $P < 0.05$) breeding when considering all nest boxes. No native species bred in the large entrance nest boxes in the 2012 breeding season. b. The proportion of nest boxes occupied by cavity nesting birds in the small and large entrance nest boxes by native species (great tits and house sparrows) during the 2011 (Fisher's Exact Test p = 0.53), 2012 (Fisher's Exact Test p = 0.07), and 2013 (Fisher's Exact Test p = 0.41) breeding when considering only available nest boxes, those not occupied by other species. No native species bred in the six unoccupied large entrance nest boxes in the 2012 breeding season.

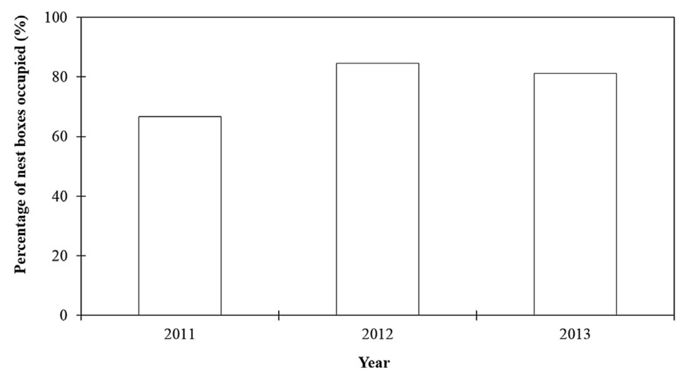

Fig. 2. The proportion of nest boxes occupied by alien species (common mynas and rose-ringed parakeets) in the large nest boxes during the 2011, 2012, and 2013 breeding seasons.

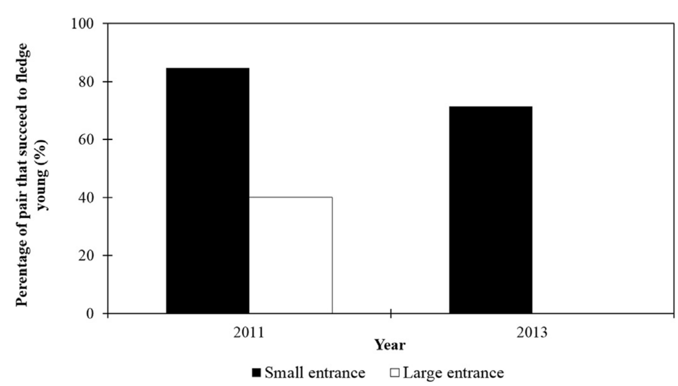

Fig. 3. Comparison between the number of great tit pairs that succeeded to fledge at least one young in the small and large entrance nest boxes in 2011 (Fisher's Exact Test p = 0.10) and 2013 (Fisher's Exact Test p < 0.05).

there was a single breeding attempt by a Scops owl observed in this study that failed, in which all the nestlings were found dead with peck marks at 2.5 weeks old under a freshly built active myna nest.

4. Discussion

Very few studies (Strubbe and Matthysen, 2009) have shown through experimentation rather than observation alone, the negative effects of nest site exploitation competition by alien species. We found that the two common alien species (common myna and rose-ringed parakeet) in the study area occupied over three quarters of the large-entrance nest boxes, leaving only a limited number of these nest boxes available for the native species. More native species in general, and great tits specifically, bred in the small rather than large-entrance nest boxes. This was not out of a preference for small-entrance nest boxes but because more small-entrance than large-entrance nest boxes were available to breed in (not occupied by other species).

In addition to exploitation competition, we presented observational data of myna expelling great tits from nest boxes, which indicate the possibility of interference competition. The breeding success of great tit pairs breeding in the large entrance nest boxes was also lower than in pairs breeding in the small-entrances nest boxes. Lower breeding success by great tits breeding in the large entrance nest boxes was due to pairs that failed completely (did not fledge young) due to usurpation by the alien common myna, such as our finding of great tit eggs and dead tit nestlings under freshly-built active myna nests.

The effects of exploitation competition may be large, and small native species may not breed altogether in locations where nest sites are unavailable due to alien species occupying all available breeding holes. In 2004, 2005 a study of cavity nesters in the same area which used large-entrance nest boxes only found that 80% of the nest boxes were occupied, of which common mynas occupied 33% of nest boxes in 2004 and 45% in 2005. Great tits in that study comprised of less than 2% of all breeding attempts (Orchan, 2007; Orchan et al., 2013). The lower number of great tits breeding in this earlier work compared with the present study is likely due to the fact that the nest boxes in the former study were all large-entrance boxes already occupied by larger species, leaving the small great tits without nest boxes in which they could breed safely.

In locations such as the Eastern Mediterranean where very few natural cavities occur due to the very limited number of old growth large trees, small-entrance natural cavities are limited since woodpeckers and rose-ringed parakeets frequently enlarge existing cavities in order to make them accessible (Charter et al., 2010a, Orchan et al., 2013). This becomes more significant with the increase in cavity nesting alien species populations, which in Israel have substantially expanded throughout the country in the past twenty years (Holzapfel et al., 2006; Yom-Tov et al., 2012).

Nest site competition seems to be dependent on the body size of competitors (Dhondt, 2011), with larger species typically are dominant over smaller ones. When alien species are significantly larger than the native species (Strubbe and Matthysen, 2009; this study), the latter may be reduced or excluded from breeding altogether due to the exploitation competition. To date most studies have been observational where alien and native species are similar sizes, some of which showed negative effects (Pell and Tidermann, 1997; Grarock et al., 2013a) and others not (Czajka et al., 2011). It is difficult to study competition in similar sized species because it is more challenging to limit the cavity resource by reducing the entrance size and prevent the aliens from breeding while allowing the native birds to continue breeding. Where relevant, there is need for more studies using experimental approach by either blocking entrances of alien species, as per Strubbe and Matthysen (2009) or using restrictor plates that reduce the entry size (as done in this study).

In comparison to exploitation competition, the effect of interference competition in breeding birds has been less studied due to difficulties in manipulating breeding birds and low sample sizes (Dhondt, 2011). Interference competition could be intense with pairs failing altogether (Goldshtein, 2013) and, as found with this study, 78% of great tits pairs breeding in the large-entrance failed due to supplementation by the mynas. Specifically, there is need for experimental studies designed specifically for interference competition in addition to exploitation competition.

In comparison to the study in the same region in 2004 and 2005 (Orchan, 2007; Orchan et al., 2013), which found that house sparrows occupied respectively 38% and 46% of the nest boxes (Orchan, 2007; Orchan et al., 2013), this more recent (2011–2013) study found that house sparrows only bred in relatively small numbers. House sparrows are the most common and opportunistic secondary-cavity breeders in Israel, having occupied many different nest boxes types throughout Israel in the past (Charter et al., 2010, 2011, 2010b). House sparrows have bred successfully in large numbers in similar nest boxes in the same study areas in the past (Orchan, 2007) and we therefore think that there should have been more pairs breeding. Since there were many unoccupied small-entrance nest boxes in the current study, the reduced number of breeding house sparrows in 2011–2013 (this study) compared to 2004–2005 (Orchan, 2007) is not due to a lack of nest sites but, we speculate, probably due to the effect of competitive exclusion between house sparrows and the larger alien species. The decline in breeding sparrows in nest boxes may also be related to changes in the numbers of common myna that was first reported in the Yarkon Park in 1997 and has since expanded its range across the country (Holzapfel et al., 2006; Yom-Tov et al., 2012). In their native range in India, common mynas were suggested to have a negative effect on native house sparrows (Khera et al., 2010) and a similar effect may have been occurring in Israel in recent years. In addition to competition for nest sites, native house sparrows and alien common mynas may also compete for food, as found in Peck et al. (2014), which found the presence of alien rose necked parakeets significantly reduced feeding rates and increased vigilance among native birds. Aggressive behaviours by aliens to natives species outside of nest cavities has been documented (Pell and Tidemann, 1997; Hernández-Brito et al., 2014) and were observed during the study chasing other, native birds (M Charter unpublished data). It is possible that these interactions could further decrease nest occupation by natives even in nest cavities the formers cannot enter but this needs to be determined in future removal experiments of alien species to determine the factors driving the decline in house sparrow populations.

In addition to active programs to control invasive alien birds by capture or other strategies (e.g., Grarock et al., 2013b), or when such control programs are not practical because the breeding populations are too large or the program is too expensive, nest boxes may provide a useful complementary strategy, providing some small native cavity breeders such as great tits with a place to breed in areas where the natural cavities are occupied by alien species. Similarly, natural cavities can be reduced in size as part of a management plan aimed at increasing the number of cavities available for great tits and reducing their need to compete with the larger aliens.

While cavity entry size manipulation could provide a useful and relatively inexpensive management strategy, other approaches will need to be devised to address the threats of alien cavity nesters to larger native species. The almost complete absence of other native cavity breeding birds in the large-entrance nest boxes in the study area, such as the larger hoopoe and Scops owls, both of which are common secondary cavity breeders throughout Israel (Charter et al., 2008, 2010b), is also of concern. Unlike great tits and house sparrows, which can be provided with nest boxes that the alien species cannot enter, hoopoes and Scops owl are similar or larger in size compared to the alien species and, therefore, it is difficult to experimentally manipulate nest boxes in order to determine whether competition exists between the larger species. In areas where there are fewer alien species in Israel, hoopoes and Scops owls breed frequently in nest boxes (Charter et al., 2008, 2010b). There is thus a need for experimental field studies focusing on interference competition between alien species and larger native species for nest sites (Grarock et al., 2013a). Further work on competition between alien and native species over other resources, such as food (Sol et al., 2011) and on the effect of nest predation by alien species on native species is important in order to better understand how alien species may limit the breeding of native species and direct future management actions.

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