

The complex interaction network among multiple invasive bird species in a cavity-nesting community

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Abstract Alien invasive species have detrimental effects on invaded communities. Aliens do not invade a vacuum, but rather a community consisting of native and often other alien species. Our current understanding of the pathways and network of interactions among multiple invasive species within whole communities is limited. Eradication efforts often focus on a single target species, potentially leading to unexpected outcomes on interacting non-target species. We aimed

to examine the interaction network in a cavity-nesting community consisting of native and invasive birds. We studied the nesting cavities in the largest urban park in Israel over two breeding seasons. We found evidence for a complex interaction network that includes negative, neutral and positive interactions, but no synergistic positive interactions among aliens. Three major factors shaped the interaction network: breeding timing, nesting preferences and the ability to excavate or widen the cavities, which were found to be a limited resource. Cavity enlargement by the early-breeding invasive rose-ringed parakeet may enhance breeding of the invasive common myna in previously unavailable holes. The myna excludes the smaller invasive vinous-breasted starling, a direct competitor of the primary nest excavator, the native Syrian woodpecker. Therefore, management and eradication efforts directed towards the common myna alone may actually release the vinous-breasted starling from competitive exclusion by the common myna, increasing the negative impact of the vinous-breasted starling on the native community. As found here, interactions among multiple alien species can be crucial in shaping invasion success and should be carefully considered when aiming to effectively manage biological invasions.

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Introduction

Introductions of non-native species into an ecosystem can lead to detrimental effects on the environment (Clavero and García-Berthou 2005; Mack et al. 2000). They also offer an opportunity to test fundamental theories and basic ecological processes shaping the establishment and spread of introduced species in new ecosystems (Lodge 1993; Sax et al. 2007). The establishment success of an alien species and its impacts are affected not only by its own traits and preferences (Shirley and Kark 2009), but also by those of the species already found in the invaded community (Elton 1958; Levine et al. 2004; Richardson 2004; Simberloff 2006; Stohlgren et al. 2003), and particularly by other alien species (Ruscoe et al. 2011). While substantial attention has been directed in the past decade towards better understanding of the establishment process of single species, less work has focused on the effect of the interactions among multiple species in the invaded community (of alien and native species) on establishment success. This is especially important as efforts to control a given species may have indirect (sometimes unpredictable) effects on non-target species in the ecosystem (Courchamp et al. 1999, 2000, 2003; Tompkins and Veltman 2006; Caut et al. 2009; Ruscoe et al. 2011). These may actually lead to additional negative impacts of the remaining untreated alien species on the native community (Soulé et al. 1988; Palomares et al. 1995; Crooks and Soulé 1999; Zavaleta et al. 2001; Caut et al. 2007; Rayner et al. 2007; Le Corre 2008; Bergstrom et al. 2009; Ritchie and Johnson 2009, Ruscoe et al. 2011).

The removal of apex predators or strong alien competitors may impact local communities, thus indirectly positively impacting other alien species. This may consequentially have detrimental effects on conservation efforts (Ruscoe et al. 2011; Ritchie and Johnson 2009). For instance, in New Zealand, the removal of invasive possums led to a significant increase in the number of invasive rats (Ruscoe et al. 2011). The release from competition for food has been proposed as the mechanism behind this increase (Sweetapple and Nugent 2007; Ruscoe et al. 2011). Relatively little attention has been directed to empirically examine the impacts of interactions among different alien and native species on establishment of alien populations (Caut et al. 2007; Trewby et al. 2008). Romanuk et al. (2009) used a simulation

approach to integrate an interaction network based on species traits into invasion models. They found that both species traits and the trophic interactions between species can influence invasion success (Romanuk et al. 2009). Thus, better understanding of the interaction network among alien species invading a single community is important for conservation efforts (Ruscoe et al. 2011; Ritchie and Johnson 2009).

Empirical studies examining the interactions among alien species and their effect on establishment success have mostly focused on negative interactions, such as predation and competitive exclusion (e.g., Elton 1958; Moulton and Pimm 1983; Simberloff and Boecklen 1991; Ruscoe et al. 2011). However, at least four types of interactions between individuals of different species within a community can occur, all of which may affect the invasion outcomes. The major interaction types include: negative ($-/-$) (e.g., aggressive behavior following competition over a resource and affecting the fitness of individuals), positive ($+/+$), neutral (with no clear effect on fitness; $0/0$), and positive/negative (\pm) relationships, in which one species benefits from the interaction while another loses as a result of the interaction, also called contramensalism (Hodge and Arthur 1996; see Table 1 in Simberloff and Von Holle 1999). Other potential interactions are positive/neutral ($+/0$) and negative/neutral ($-/0$). Simberloff and Von Holle (1999) proposed that positive (synergistic) interactions among different alien species are potentially more important than previously recognized.

While positive interactions in plants have received attention in facilitation studies (Brooker et al. 2008; Callaway 2007; Thorpe et al. 2011), relatively little empirical work has examined the interaction network of animal communities that consist of several native and introduced species. Most studies addressing the interactions between alien species that included animals concentrated on interactions between species belonging to different trophic levels (e.g., a plant and its pollinator/dispersal agent, predators and prey or parasite and host; Grosholz 2005; Nuñez et al. 2008; Simberloff and Von Holle 1999). If we aim to predict invasion results and to manage them effectively, it is essential to understand the interaction network among alien species and among the aliens and their native counterparts at a whole community level in the framework of one study (Simberloff 2006; Ruscoe et al. 2011), which was the goal of this study.

The cavity-nesting bird community

In animals, the examination of the interaction network at a whole community scale is often difficult. However, cavity-nesting birds provide a good opportunity to test such complex networks (Aitken and Martin 2008; Blanc and Walters 2007, 2008), comprising of a clearly defined community where species potentially use and interact over the same resource—the nesting cavities (Martin et al. 2004; Newton 1994; but see Wesolowski 2007). In many cases, a small proportion of cavity-nesting bird species, mainly woodpeckers (*Picidae*), are the major engineers of cavities. They are thus termed primary excavators (Newton 1994; Drever et al. 2008). The majority of cavity-nesting species cannot excavate their own nests. These are called secondary cavity-nesters and they rely on available woodpecker-built cavities, on natural cavities generated by insects, fungal decay and other processes or on human-made cavities. Some bird species cannot excavate a cavity alone, but can enlarge or alter available cavities, especially in soft timber (Martin et al. 2004), they are called weak excavators. The variability among the cavity nesters leads to a nest web of interactions among the different cavity-nesting birds within a given community (Blanc and Walters 2007, 2008; Martin and Eadie 1999).

Cavity-nesting species can differ in their cavity preferences (Martin et al. 2004) and many interactions occur around the cavity resource (e.g., during selection of cavities and competition over them; Blanc and Walters 2008). For example, the cavity entrance size determines which nesting species and/or predators can enter and use the nests (Remm et al. 2006; Wesolowski 2002). Moreover, cavities are often a limited resource (Albano 1992; Orchan 2007; Rendell and Robertson 1989; Van Balen et al. 1982; Wiebe 2001, but see Wesolowski 2007), especially in urban habitats, due to uprooting of decaying trees (Davies et al. 2009; Newton 1994). The availability of cavities is known to determine breeding densities (e.g., Orchan 2007; Strubbe and Matthysen 2007; but see Wesolowski 2007) along with the interactions among the cavity-nesting species (Martin et al. 2004). Since many introduced bird species often tend to first establish in human-dominated areas (Chiron et al. 2009; McKinney 2006), and particularly in urban parks (Case 1996), cavity availability can have much impact on the potential of alien cavity-nesting species

to establish successfully (Pell and Tidemann 1997; Strubbe and Matthysen 2007), and eventually on their impacts on the native community. Cavity-nesting communities are comprised of a hierarchy of users that interact both directly and indirectly (Blanc and Walters 2008). In an earlier study, Orchan (2007) found that nesting holes are a limited resource in the study area.

In this study, we aimed to study the interaction network between three alien and four native cavity-nesters during the breeding season. Following detailed field work, we constructed the interaction network within the cavity-nesting bird community in a large urban park, the Yarkon Park, by examining the breeding behavior of the cavity-nesting species in the area. While this community is large enough to show complex interactions over the cavity resource, it is small enough to enable us to construct and understand the interaction network.

Here, by exploring the cavity resource interaction network we aimed to better direct management actions including control efforts when needed, taking into account multiple species interactions and indirect effects. We predicted that alien species that are more similar in their nesting requirements (cavity characteristics and breeding season timing) will show stronger competitive interactions. We predicted that the primary excavator (the Syrian woodpecker) and the weak excavator (the rose-ringed parakeet) will facilitate both alien and native secondary cavity nesters by generating cavities and by modifying existing cavities, respectively, making them more suitable for the nesting of the other species, resulting in complex interactions within the community (Fig. 1).

Materials and methods

Study system

The study was conducted in the Yarkon Park, Tel-Aviv, the largest urban park in Israel (262 hectares; 32°02'N, 34°47'E). The Yarkon Park comprises of several sub-environments (e.g., open lawns, a non-native Tropical Garden, Eucalyptus grove and Tamarisk grove) with a range of management regimes, as detailed in Shwartz et al. (2008). Fifteen alien bird species are known to have been introduced in the park,

Table 1 Characteristics of the cavity-nesting bird community in the Yarkon Park, Tel Aviv, Israel

Common name (Latin name)	Alien/ native	Nest site characteristics	Native range	Number of broods per season	Mean incubation and nestling period (days)	First record in Tel Aviv area	Population size (2006) and trend
Rose-ringed parakeet ^a (<i>Psittacula krameri</i>)	Alien	Natural and woodpecker cavities, often enlarged. Same cavities reused in subsequent years	Northern India	1	68 (\pm 9.1) ^g (n = 24)	1963	981 \pm 401 ^g Increase
Common myna ^b (<i>Acridotheres tristis</i>)	Alien	Natural tree and wall cavities. Also in Palm trees	India, Central and Southern Asia	Up to 3	34 (\pm 5.5) ^g (n = 20)	1997	2,627 \pm 414 ^g Increase
Vinous-breasted starling ^c (<i>Sturnus burmannicus</i>)	Alien	Cavities in trees and in eaves and roofs	South East-Asia	2		2000	373 \pm 102 ^g Increase
House Sparrow ^d (<i>Passer domesticus</i>)	Native	Nest sites include woodpecker and natural cavities, palm trees, cavities in buildings	Israel and Eurasia	Up to 4	26–30 (n = 31) ^f		
Syrian woodpecker ^e (<i>Dendrocopos syriacus</i>)	Native	Self-excavated tree cavities. One pair can use several nest-cavities in one season until they successfully breed	South East- Europe, Israel and Turkey	1	35–37 (n = 13) ^f		
Great tit ^e (<i>Parus major</i>)	Native	Tree and woodpecker cavities or in man-made structures including pipes, and cavities in walls	Western Palearctic	2	30–35 (n > 50) ^f		
Scops owl ^e (<i>Otus scops</i>)	Native	Tree cavities, buildings	Central West Palearctic, wintering in Central Africa and South Asia	1	46–47 (n = 22) ^f		

Mean incubation and nestling period refers to the total number of days between first egg laying and the last nestling to leave the nest

^a Cramp and Perrins (1994), Shirihai et al. (1996), Shwartz et al. (2009)

^b Hatzofe and Yom-Tov (2002), Holzapfel et al. (2006), Feare and Craig (1999)

^c Lin (2001), Feare and Craig (1999)

^d Kark et al. (2007), Cramp and Perrins (1994), Shirihai et al. (1996)

^e Cramp and Perrins (1994), Shirihai et al. (1996)

^f Shirihai et al. (1996)

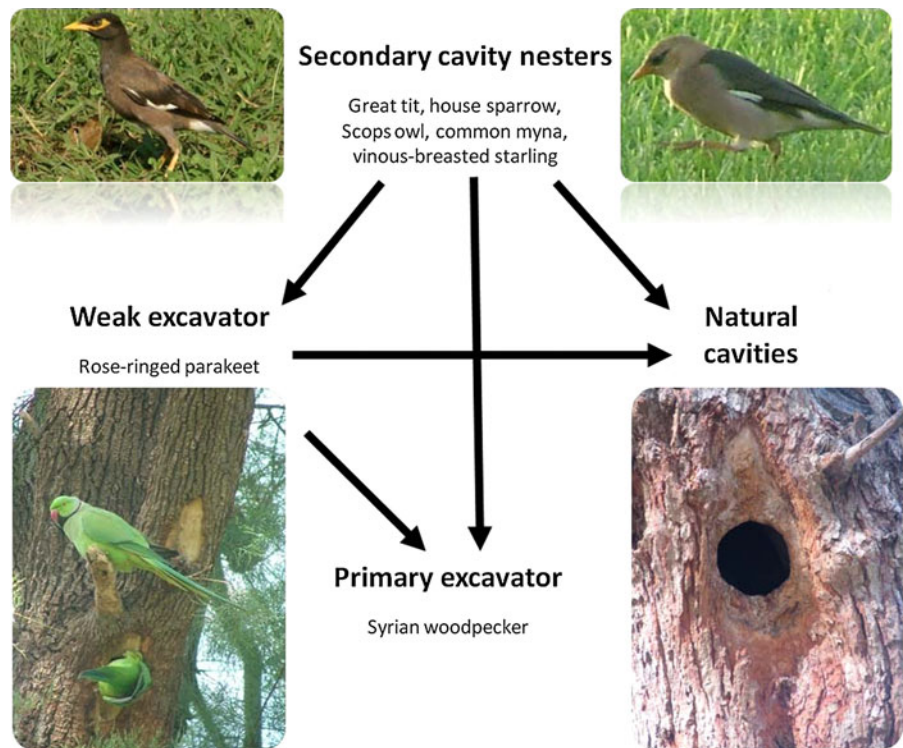
^g Calculated from data collected in this study (2006)

most of them since 1997 (Shwartz et al. 2008). Four species have established reproducing populations of more than 150 individuals in the Yarkon Park. Of these, three alien invasive species nest in natural cavities or in cavities constructed by woodpeckers (Table 1). These include the rose-ringed parakeet (*Psittacula krameri*), the common myna (*Acridotheres tristis*) and the vinous-breasted starling (*Sturnus burmannicus*), all originating from India/SE Asia

(Table 1). The rose-ringed parakeet is the only alien bird that can enlarge the cavity entrances to adjust them to its size, acting as a weak excavator (Kotagama and Dunnet 2007).

We found four native species nesting in cavities in the park (Table 1). These included the Syrian woodpecker (*Dendrocopos syriacus*), which is the only primary excavator in this community, the scops owl (*Otus scops*), the great tit (*Parus major*), and the house

Fig. 1 Hypothetical nest web structure in the Yarkon Park. The boxes represent the different species in the cavity-nesting bird community. Arrows represent the potential relationships between the species that is using a certain resource provided or enhanced by another species (towards which the arrow is pointed). The photos show the three most common alien cavity nesters in the community, including the common myna (*top left*), the vinous-breasted starling (*top right*) and the rose-ringed parakeet (*bottom left*) (photos by A.S.). While the cavities themselves are not part of the biotic interaction network, they are shown in the figure to clarify and emphasize their importance in the system



sparrow (*Passer domesticus*), a native urban exploiter (Kark et al. 2007). The Syrian woodpecker breeds only in cavities that it excavates and normally excavates a new cavity each year (Cramp and Perrins 1994). Following the introduction of the cavity-nesting alien birds into the park, the total number of bird species that use cavities almost doubled to seven species belonging to six families (Table 1).

Cavity detection and surveillance

Prior to the breeding season, a professional birder surveyed the study area, identifying potential breeding cavities following Pell and Tidemann (1997). The location of the cavities was recorded using a GPS device. During the breeding season of 2005 (March–August) and 2006 (February to August), we examined all the cavities in the field ($n = 290$) in order to identify their owner (the species nesting in each) and to record changes in cavity occupancy. We considered a species to be a cavity owner when it was seen for over two consecutive weeks in the cavity. In 2005, we visited each cavity once a week and observed the nest from the ground for 10 min. Occupancy was considered as a case where individuals of a given species

were recorded active in the cavity or where nestlings call or eggs were seen. When necessary, in order to identify the nest owner, we climbed up to the nest using professional climbing gear. During the second study year (2006), we climbed to the cavities on a weekly basis and monitored the nests closely, using a small infra-red camera. During each visit, we identified the species nesting in the cavity and recorded evidence for breeding material, eggs, nestlings or fledglings in the nest.

We conducted point counts of the alien species using the Distance Sampling method for population size estimates following Buckland et al. (1993, 2004), as detailed in Shwartz et al. 2008. We used fixed 100 m radius circular plots. Before beginning each survey, we waited for 5 min at the point as a “calming period”. Following this, we sampled all the birds seen or heard for 10 min. During each sampling period, we recorded all bird species, the number of individuals, and the distance from the observer using small flags positioned using a rangefinder (Leica Rangemaster LRF 900) every 10 m from the center point.

For the rose-ringed parakeet, which cannot be counted reliably in the park using point counts, estimates are based on roost counts. Population size

trend between 2003 and 2006 is based on our counts (Orchan 2007; Shwartz et al. 2008).

Estimating nest site characteristics

In order to compare the cavity preferences among species, at the end of each breeding season, we measured 20 variables (listed below) that quantify the cavity hole, cavity tree and cavity site characteristics following Newton (1994) and Martin et al. (2004). The cavity characteristics examined included: cavity depth (cavity entrance to bottom edge), cavity entrance length (height) and width, cavity entrance area (calculated as an ellipse), tunnel length, inner space diameter and cavity height above ground. We assessed the cavity age for woodpecker cavities when detectable and recorded whether the cavity was excavated by the Syrian woodpecker or was generated by other decay processes. We also assessed whether the rose-ringed parakeet enlarged the entrance of the cavity, as they often do in both native and introduced ranges (Strubbe and Matthysen 2007). We identified enlarged cavities by the shape and color of the cavity edge. Cavities with sharp-edges and light-colored edges were considered to be new, while those with soft edges and dark color edges were considered older cavities. We measured the following cavity tree characteristics: circumference at cavity height, tree height (measured using a clinometer) and recorded the tree species. Site characteristics included the number of trees and number of additional cavities located in a radius of 10 m from each cavity. We also measured the distance of each cavity to the nearest other cavity, its distance to the nearest permanent water source, its distance from nearest walking trail and its distance to the nearest park boundary, which also reflects the distance from built up areas. This was done using ArcGIS 9.2 (ESRI 2004).

Identifying the interactions between cavity-nesting species

We used the following cavity characteristics preferences, breeding timing and cavity occupancy data to identify potential negative, positive or neutral interactions in the cavity-nesting community of the Yarkon Park.

1. Cavity preference similarity: we first explored whether the cavity-nesting species are similar in their cavity preference using an analysis of variance (ANOVA) for the occupied cavities. We checked for multicollinearity among the different cavity variables examined and measured. As some variables showed significant covariation, we selected for the model the seven variables which showed the lowest autocorrelation and which we predicted will play important role in cavity selection of all species (following Paclik and Weidinger 2007; Table 2). We then used a cluster analysis with an average linkage between groups (Everitt and Landau 2001) to examine similarities among the different species in their cavity characteristics (Fig. 2). Only the significant variables were included in this analysis (Table 2). We assumed that higher similarity in cavity preference may indicate stronger potential of competition and therefore can help in identifying potential negative versus neutral interactions.
2. Breeding timing: we explored shifts in the breeding timing of each species and the distribution of the number of nesting attempts over the breeding season. During each week of the 20-week breeding season (in both 2005/6), we summed the number of nesting attempts, standardized it with the total number of nesting attempts of each species (Fig. 3) and tested the correlation among species. Significant positive correlation can indicate that two species have the same nesting timing and therefore have higher potential of competing with each other.
3. Cavity ownership and replacement: during each of the two breeding seasons, we recorded any change in cavity ownership among the different species. We defined a “replacement” of ownership as a case where while one species showed signs of breeding activity in a given nest (e.g., nesting material, eggs or chicks), it was replaced in the same cavity during its nesting or immediately after the fledgling stage by another species. We did not consider a case as a replacement, if a nest was inactive for over 2 weeks and was later occupied by another species. Replacement while breeding was considered as a negative interaction between species.

Table 2 Cavity, tree and nesting site preferences of cavity-nesting birds in the Yarkon Park, Israel (2005, 2006 seasons)

Nesting site variables Mean (CV)	Syrian-woodpecker (n = 10)	Rose-ringed parakeet (n = 45)	House sparrow (n = 50)	Common myna (n = 35)	Vinous-breasted starling (n = 13)	Difference between species
<i>Cavity characteristics</i>						
Height above ground in m	4.2 (71)	6.6 (42)	4.8 (58)	5.9 (44)	4.0 (41)	$F_{4,147} = 4.4^{**}$
Entrance area size (cm ²)	66 (16)	133 (83)	133 (85)	215 (81)	73 (18)	$F_{4,147} = 9.7^{***}$
Cavity depth (cm)	31 (77)	34 (43)	30 (52)	24 (33)	22 (26)	$F_{4,146} = 3.6^{**}$
<i>Tree characteristics</i>						
Tree circumference (cm)	92 (32)	135 (43)	127 (60)	127 (49)	100 (39)	$F_{4,147} = 0.7$ NS
Tree density (10 m radius)	2.6 (86)	2.9 (84)	2.6 (79)	2.1 (69)	3.1 (89)	$F_{4,147} = 0.7$ NS
<i>Site characteristics</i>						
Intensity of management	2.8 (44)	2.6 (37)	3.0 (34)	2.2 (34)	2.5 (41)	$F_{4,146} = 0.5$ NS
Distance to water (m)	89 (20)	15 (46)	34 (29)	27 (38)	66 (19)	$F_{4,147} = 7.4^{***}$

We show the mean of nesting site variables for each species and the coefficient of variation in parentheses (=SD/mean in %). The sample size (n) is the number of cavities measured. The great tit and scops owl are not included here due to the small sample size

* $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$

NS-non significant

In order to understand the potential positive effect of the primary excavator (Syrian woodpecker) and secondary excavator (rose-ringed parakeet), we explored the preferences of all species for nesting in woodpecker made cavities and in cavities enlarged by the secondary excavator, the rose-ringed parakeet. We built for each species generalized linear models with a binomial error structure (logit link function) in order to explore (1) preference for woodpecker-built versus natural cavities, (2) preference for cavities enlarged by parakeets and the interaction of the two variables (Table 3). We identified interaction as positive when one of the two excavating species (Syrian woodpecker and rose-ringed parakeet) facilitated breeding conditions for other cavity-nesting species (e.g., when a given cavity nester has a significant tendency to nest in woodpecker-built cavities and/or in cavities enlarged by the alien parakeet).

Inter-specific behavioral interactions

In order to complement our understanding of the cavity preferences, we recorded the interaction among species in the first breeding season applying dedicated behavioral observations in the field. We examined the nest ownership dynamics at the species level, and both the inter- and intra-specific behavioral interactions in

the vicinity of the nest, following Pell and Tidemann (1997). Once a week, between March and August 2005, in addition the regular cavity monitoring explained above, we observed the 153 active cavities from a 50 m distance for 10 min (after allowing a 5-min calming period upon arrival in the area). We divided the interactions of individuals of one species towards another into several types: negative (aggressive) interactions, positive (cooperative) and neutral interactions. Aggressive interactions included distinct aggressive calls and behaviors such as directly flying at another bird or when physical contact was apparent. If the attacked bird left its position, it was recorded as 'losing' the encounter. In the case of fights over cavities, we recorded the species that was evicted as a loser whenever the outcome was clear (Pell and Tidemann 1997). If an aggressive behavior was recorded within the recording period, we continued watching the interaction until it ceased in order to record its outcome. Neutral inter-specific interactions were defined as cases where the owners of the nest and individuals of another species were both near the nest, but did not act (physically or vocally) in a noticeable fashion towards each other. This behavior was observed when two species nested in close proximity, sometimes in the same tree. Positive behavioral interactions near the cavity were cases where

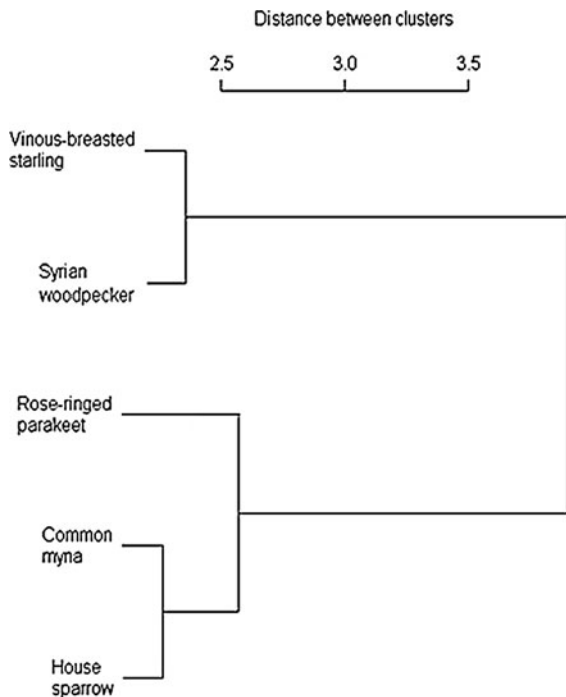


Fig. 2 Dendrogram showing results of a cluster analysis used to group cavity-nesting bird species as per Martin et al. (2004) (Fig. 3) and on the basis of similarities in cavity characteristics (see Table 2). The least similar clusters have the greatest distance between splitting branches (see presented scale). Analysis included all species for a total of 153 cavities (2005), data are in Table 1. The great tit and scops owl are not included in the figure due to small sample sizes

individuals of different species were cooperating (e.g., joint mobbing of individuals of two different species on another individual).

Data analysis

All statistical analyses were performed in R software v 2.6.0 (<http://www.R-project.org>). A GLM model was used to compare species hole type preference (Table 3). An ANOVA was used to compare mean nest preferences of species (Table 2). For both the GLM and ANOVA models, we tested for compliance with model assumptions, normality and non-constant error variance using Kolmogorov–Smirnov and Levene’s tests (Zar 1999). We used cluster analysis (Everitt and Landau 2001) to compare species’ breeding preferences using the estimated nest site characteristics measured. To highlight the breeding timing, a third order polynomial relationship was fitted

to the sum of active nests (per week) for each of the bird species studied. Pearson’s correlation coefficient was used to calculate the correlation of the weekly sum of active nests per species.

Results

Cavity occupancy

Over the two study seasons combined, we located a total of 290 cavities in the study area. After climbing up to the cavities, we found that 43 of the cavities were unsuitable for nesting, being either flooded after the rain, too shallow or too small. This left a total of 247 cavities suitable for nesting in the area. The community of cavity-nesting bird species occupied 100 woodpecker-built cavities (73 % of the 137 suitable woodpecker-built cavities available) and 92 natural cavities (83 % of the 110 suitable natural cavities recorded in the study area). The cavity density in the study region was 0.7 cavities per hectare. Over the two study years, we recorded 254 nesting attempts (some cavities were used multiple times over the same season). Nesting attempts by alien birds were recorded in 63 % of the occupied cavities. Cavities with multiple nesting attempts always involved an alien bird species in at least one of the attempts. Eleven trees (16 %) had more than one cavity available for nesting. In ten of these 11 trees, two different species bred simultaneously, and these always included the native urban exploiter (Kark et al. 2007)—the house sparrow (either with the common myna or the rose-ringed parakeet). The number of breeding attempts in the cavities is shown in Fig. 3. Surprisingly, no breeding attempt was recorded for the great tit over the whole study period and only one breeding attempt was recorded for the scops owl in our study area. We therefore excluded these two species from most statistical analyses, as sample size was too small. However, we refer to these findings in the Discussion.

Nesting site characteristics

The cavity-nesting species in the Yarkon Park showed significant differences in their cavity preference and site characteristics, but not in the characteristics of the breeding trees (Table 2). Based on the cluster analysis,

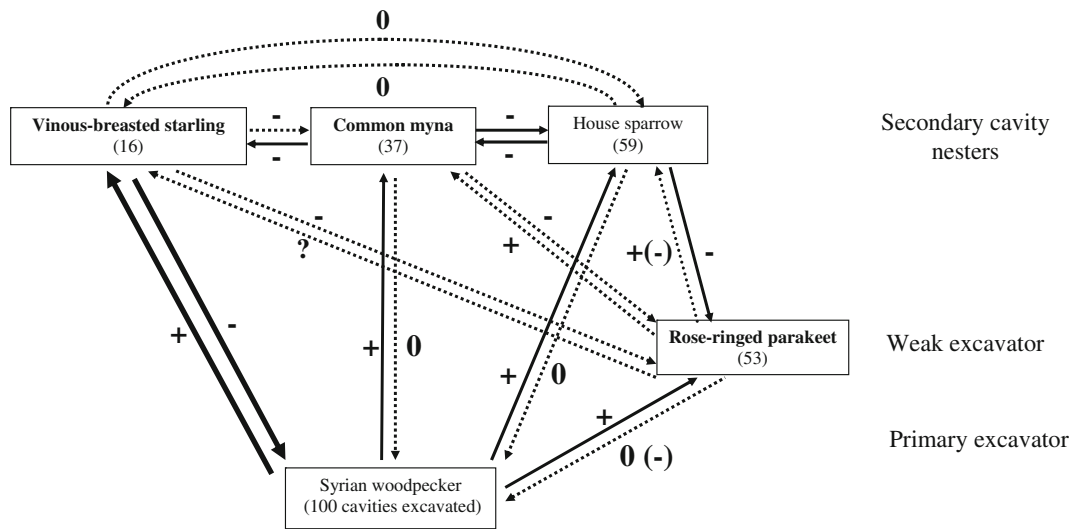


Fig. 3 Estimated cavity nest web diagram (following Martin and Eadie 1999) showing cavity use interactions of both the native and the alien (in *bold*) bird species of the Yarkon Park. The number of nesting attempts recorded for each species is marked in parentheses. The *arrows* are pointed from the source of the effect towards the recipient. Arrow width is proportional to the proportion of cavities of each type used (under or over 50%). The integrated interaction type is marked by + (positive), 0 (neutral) and - (negative) signs. For example, + is a case where individuals of the recipient species benefit from the presence of the source species, while 0 is a case

where the source species is not known to affect individuals of the recipient species in relation to the cavity resource. Relationships are based on integration of the species cavity preference, timing of breeding, nest replacement during the breeding season and the behavioral interactions. Cases where the interaction differs between these criteria have two marks. For example, cases where the interaction is positive based on one criterion and negative based on another are marked as +(-). Uncertain or non-significant relationships are marked with a dashed line or question mark. The great tit and scops owl are not included in the figure due to small sample sizes

Table 3 Proportions of nesting attempts per species by cavity type (woodpecker built or natural hole) and entrance types (enlarged or unenlarged) in the Yarkon Park (2005/2006)

Cavity type	Enlargement	Syrian woodpecker (11)	Vinous-breasted starling (16)	Common myna (37)	House sparrow (59)	Rose-ringed parakeet (52)	Total number of cavities
Woodpecker-built cavity	Enlarged	9 % ns	6 % ns	14 % ns	19 % ns	44 % ***	64 (A)
	Unenlarged	91 % ** (A)	75 % *** (A)	8 % ns	24 % ns	6 % ns	65
Natural cavity	Enlarged	0 % ns	0 % ns	11 % ns	5 % ns	27 % ***	17 (B)
	Unenlarged	0 % ns	19 % ns	68 % *** (A)	53 % * (A)	23 % ns	97

Sample sizes for each species are shown in parentheses. A denotes significant preference for the use of cavities built by the Syrian woodpecker (vs. natural cavities), and B denotes significant preference for enlarged (vs. unenlarged) cavities

* $p < 0.05$; *** $p < 0.001$; ns non-significant, and (N) is the total number of nesting attempts. Note that multiple nesting attempts can occur in the same cavity. Therefore, the sum of nesting attempts in a given cavity type is not equal to the total number of cavities

the cavity-nesting community can be divided into three groups (Fig. 2). The first group consisted of (1) the alien vinous-breasted starling and the native Syrian

woodpecker. Both species used the cavities with the smallest entrance area and the lowest cavities (in terms of their location on the tree) compared with the other

species (Table 2). The second group included the alien common myna and the native house sparrow; both birds used the cavities with the largest entrance size (Table 2). These diverged from the secondary excavator—the rose-ringed parakeet. The parakeets occupied the highest and the deepest cavities of all species, generally located closer to water sources, mainly along the Yarkon River.

Overall, cavities were found in 11 different tree species, most of which have been planted in the urban park and are alien to the region. Cavities mainly occurred in eucalyptus (*Eucalyptus camaldulensis*; 54 % of all cavities) and tamarisk (*Tamarix aphylla*; 18 %) followed by the Australian she-oak (*Casuarina equisetifolia*; 9 %), poplar (*Populus euphratica*; 8 %) and other tree species (11 %). The rose-ringed parakeet showed significant preference for breeding in eucalyptus (80 % of parakeet nests were in eucalyptuses, $\chi^2 = 18.6$, $df = 4$, $p < 0.01$). The Syrian woodpecker showed significant preference for tamarisk ($\chi^2 = 16.7$, $df = 4$, $p = 0.01$).

Among the natural ($n = 92$) cavities and woodpecker-built ($n = 100$) cavities that were occupied in the study area, we were able to identify that 63 cavity entrances (11 natural and 52 woodpecker-built cavities) were enlarged by the rose-ringed parakeet (33 %) and 122 were left intact (64 %). The parakeets showed significant preference for enlarged cavities compared with unenlarged ones in both natural and woodpecker made cavities (Table 3).

The parakeets enlarged 88 % of the cavities they used for breeding. The common myna and the house sparrow did not show significant preference for enlarged cavities and used them at a proportion of 20 % for the myna compared with 33 % available in the park ($p = 0.11$) and 27 % for the house sparrow (34 %, $p = 0.40$). In contrast, the vinous-breasted starling almost exclusively occupied intact (non-enlarged) cavities (92 % of all cavities used, $p = 0.04$).

The two alien Sturnids (the common myna and the vinous-breasted starling) differed in their cavity type preferences. While the vinous-breasted starlings were found mainly in intact woodpecker-built cavities (Table 3), the common myna nested significantly more often in natural un-enlarged cavities (Table 3). The house sparrow did not show a statistically significant bias for a certain cavity type (Table 3). Additionally, both the common myna and the house

sparrow also used human-made infrastructure for nesting (e.g., buildings and sculptures), which were not included in the analyses here.

Timing of the breeding season

The timing of the breeding season in the park differed among some of the cavity-nesting species (Fig. 4). The house sparrow, common myna and vinous-breasted starling showed a peak in nest occupancy in the end of April and early May. The rose-ringed parakeet was the first to start the breeding in February and had only a single, long breeding cycle per pair throughout its breeding season (Fig. 4). Additionally, the rose-ringed parakeet was the only species in which all nests were active at the same time. Its breeding season was not significantly correlated with the other cavity-nesting species breeding in the park (house sparrow $r = -0.02$, ns (2005), vinous breasted starling $r = -0.38$, ns (2005), $r = 0.17$, ns (2006), Syrian woodpecker $r = -0.28$, ns.(2005), except for significant correlation between the nesting season of the rose-ringed parakeet and the common myna in 2005 ($r = -0.56$, $p < 0.01$, which was not found in 2006 ($r = 0.08$, ns). The next species to start breeding following the parakeet was the house sparrow, which had a long breeding season with multiple breeding cycles (Table 1; Fig. 4). Its breeding cycle was strongly correlated with the cycle of the two alien starlings in 2005: with the common myna ($r = 0.53$, $p < 0.01$) and with the vinous-breasted starling ($r = 0.73$, $p < 0.001$). It was also significantly correlated with the breeding cycle timing of the Syrian woodpecker in 2005 ($r = 0.51$, $p < 0.05$). The breeding cycle of the common myna was strongly correlated in timing with the vinous-breasted starling ($r = 0.80$, $p < 0.001$ in 2005 and $r = 0.93$, $p < 0.001$ in 2006). Both Sturnids, originating from the same region, had multiple attempts over the breeding season (Table 1) and about 80 % of their breeding attempts occurred in the same period. The breeding season of the alien common myna began 3 weeks earlier than the alien vinous-breasted starling. Importantly, the breeding season of the native cavity engineer, the Syrian woodpeckers, coincided with all other bird species except the rose-ringed parakeet ($r = -0.28$, ns in 2005). The peak of the breeding season of the woodpeckers in early June matched that of the two alien Sturnids (Fig. 4), as the early-breeding alien

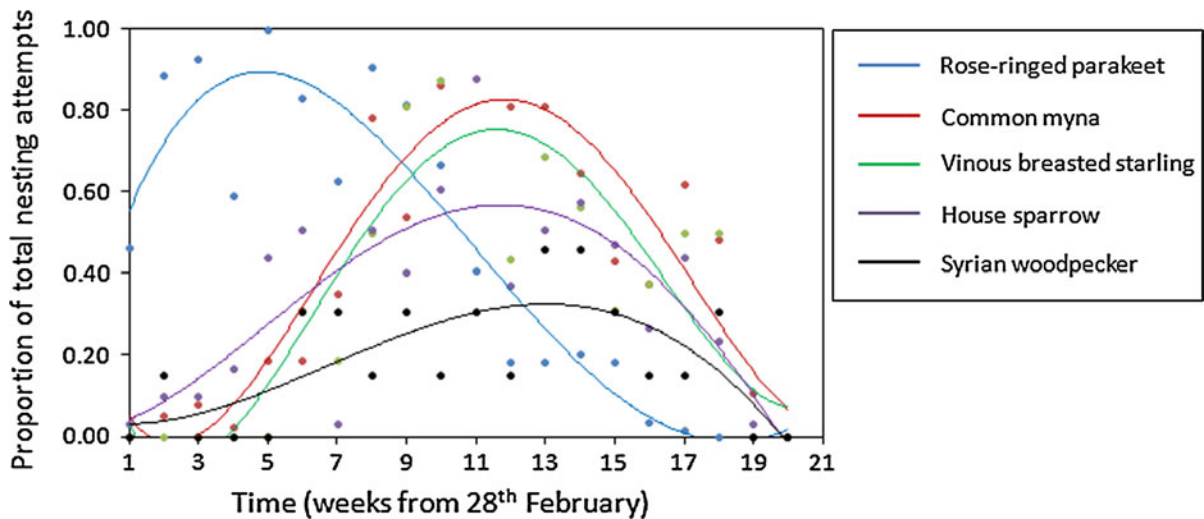


Fig. 4 Breeding timing dynamics of the cavity-nesting species of the Yarkon Park during the 2005 and 2006 breeding seasons. Points represent the weekly proportion of nesting attempts per species and lines show the trend (third order polynomial curve). The alien rose-ringed parakeet begins its breeding earlier than all the other cavity nesting species in the park. The alien common myna and vinous-breasted starling's breeding timing overlap. The native Syrian woodpecker and house sparrow both have long breeding periods that partly overlap with those of all the alien species. The proportion of nests that are during the

parakeet was approaching the end of its breeding season (only 30 % of all parakeet breeding attempts occurred at that time).

Behavioral interactions among species

In the first breeding season, we conducted 1,006 behavioral observations of active (occupied) cavities. In 528 occasions we recorded activity around the cavity during our observations, including interactions and parental care provision for eggs and nestlings. Of these, we recorded 63 intra- and inter-specific interactions between cavity owners and birds of other species, of which 73 % ($n = 46$) were aggressive. Seventeen aggressive interactions around the cavities (37 % of all 46 aggressive interactions) were initiated by the common myna. The vinous-breasted starling and the house sparrow initiated 18 % of the aggressive interactions (7) each and the rose-ringed parakeet initiated 11 % (9 interactions). In all cases where we recorded common mynas initiating aggressive behavior towards the native house sparrows, the sparrows eventually abandoned their nest before completing their breeding cycle ($n = 4$). Eleven of the common

same time changes among species. While the majority of the nests of the rose-ringed parakeet (0.87) are active during the same time (week 5), only 0.45 and 0.3 of the nests of the house sparrow and Syrian woodpecker, respectively, are active at the same time. The common myna and vinous-breasted starling's breeding seasons peak in week 12, when 0.82 and 0.78, respectively, of the nests are active. The great tit and scops owl are not included in the figure due to small sample sizes. All cavity types are pooled in the figure. This figure is best viewed in color

myna interactions recorded included attacks on rose-ringed parakeets in their cavities while the parakeets had either eggs or nestlings in the nest. Of the seven interactions involving the vinous-breasted starling, five were with Syrian woodpeckers in their nests. In two of these cavities the vinous-breasted starling replaced the Syrian woodpecker within less than a week from the interaction day. The interactions between the vinous-breasted starling and the Syrian woodpecker and between the vinous-breasted starling and the common myna were especially aggressive and included much physical contact between the interacting birds. Interestingly, we did not spot any aggressive interactions between cavities owners of different species in trees that had two or more simultaneous breeding attempts in different cavities on the same tree. We reported this as cases of neutral interactions. We did not record positive behavioral interactions between different species around the nesting sites.

Cavity replacements over the breeding season

Over the two study seasons, we recorded 22 replacements of cavity ownership during or immediately

following the breeding cycle. The invasive common myna replaced the rose-ringed parakeet five times immediately after the parakeets ended the breeding cycle. These replacements involved aggressive harassment of the nesting parakeet pairs by the common mynas during their breeding. In four of the five cases where the common myna replaced the house sparrows, the sparrows did not manage to complete their breeding cycle due to aggressive replacement by the myna. The native house sparrow replaced the rose-ringed parakeet seven times by filling up the parakeet cavity with nesting material, while the rose-ringed parakeet replaced the house sparrow twice during the breeding cycle, while the sparrows started bringing nesting material into the cavity. The vinous-breasted starling replaced nesting Syrian woodpeckers twice before the latter completed their breeding cycle, and replaced the locally rare scops owl once.

Discussion

Understanding the interactions among multiple alien and native species is important for effectively prioritizing future conservation and control efforts and resources for mitigating invasive species impacts (Ruscoe et al. 2011). Among birds belonging to the cavity-nesting community of the Yarkon Park, we found evidence for a complex network of interactions. These interactions operate between native and alien species as well as among different alien species. The majority of the interactions among species that have partly overlapping breeding preferences were negative (Tables 2, 3; Fig. 2). Neutral interactions were seen among species with varying nest site preferences (Fig. 2) and/or with unparalleled breeding seasons (Table 3; Fig. 4), such as the common myna and the Syrian woodpecker. Contramensalism (\pm) occurred where woodpeckers facilitated the breeding conditions of secondary cavity nesting species and especially that of the vinous breasted starling and the rose-ringed parakeet (Fig. 3).

The most complex interactions occurred between the alien common myna and rose-ringed parakeet, which co-occur and are sympatric in their native India and South East Asia. This involved both negative and positive influences. The two species showed aggressive behavioral interactions around active breeding cavities. These negative interactions were mainly

characterized by aggressive fights over cavities, a behavior which was also observed in their native range (Dhanda and Dhindsa 1996). Sixty five percent of the aggressive interactions initiated by the common myna in our observations were against rose-ringed parakeets. However, the common myna benefited from this secondary excavator by using holes that were widened by the parakeets. While the mynas did not show statistically significant preference for the widened cavities (possibly due to low power resulting from relatively limited sample sizes), the availability of cavities that were suitable for mynas apparently increased due to the enlargement of small entry cavities by parakeets. These were otherwise not accessible to common mynas, as they were probably too small to enter (Dhanda and Dhindsa 1996). This finding may be important, as cavity nests seem to be a limited resource in the park, as discussed below. While the widened cavities were often occupied early in the season by the parakeets, making them unavailable for the mynas, we found that more than half of cavities that were used consecutively in the same season (5 of 9) were cases where the common myna replaced the parakeet after the parakeet completed its breeding. We hypothesize that the ability of parakeets to occupy the cavities earlier in the season and to protect them later (Dhanda and Dhindsa 1996; Pithon and Dytham 1999; Shirihi et al. 1996) can explain these findings. In the Yarkon Park, mynas may partly overcome the constraints imposed by the parakeets as they are generalists and can use a wide range of cavities (Dhanda and Dhindsa 1996; Feare and Craig 1999). Thus, the common mynas may successfully establish breeding populations and expand their range. Indeed, since the first common myna was observed in Israel in 1997 in the Yarkon Park, the species has expanded its range (Holzapfel et al. 2006) and is currently found in vast areas of Israel from the Upper Galilee in the north to Eilat in the south.

Although parakeets mostly nested in woodpeckers' cavities, we did not find strong interspecific interaction among rose-ringed parakeets and Syrian woodpeckers. While parakeets can enlarge and use woodpecker-built cavities, parakeet and woodpeckers differ in their cavity type preference (Table 2; Fig. 2) and their breeding seasons only partly overlap, with the parakeets beginning their breeding earlier in the season than the woodpeckers (Fig. 4). We also did not record any aggressive interactions

or replacements between these two species. Evidence from populations of parakeets in Europe reveals that parakeets can enlarge the cavities for 3 years before using them (Shwartz, A. and Strubbe, D., unpublished data). The parakeet cannot use the woodpecker cavity for nesting during the first season because its entrance or interior size is usually too small for parakeet size (Cramp and Perrins 1994; Shirihai et al. 1996; Feare and Craig 1999). Over the following year the rose-ringed parakeet starts its breeding before the woodpecker, and extensively enlarges the entrance size of the woodpecker cavity. This time delay between cavity excavation and enlargement may lead to their interaction.

Since there is a lag in time between the excavation process by the woodpecker and the breeding of the parakeet, and since woodpeckers excavate new breeding cavities annually and prefer to nest in newly build cavities (Wiebe et al. 2007), we suggest that while the woodpecker positively influences the parakeets the reverse interaction seems to be neutral. This finding from Israel is in agreement with work in Belgium, which did not find strong influence of rose-ringed parakeets on native cavity-nesting birds (Strubbe and Matthysen 2007).

Interestingly, the interaction between the aggressive common myna and the Syrian woodpecker also seems to be neutral. We did not observe any aggressive interactions or disturbance by mynas of woodpeckers around the cavities and did not record any cavity replacements between the two species. This is likely related to the fact that the common myna is too big to enter the woodpecker cavity before enlargement by parakeets and cannot enlarge the cavity by itself. This result is in contrary to the negative effect found in other studies of starlings, such as the European starling (Fisher and Wiebe 2006; Winkler 1973; but see Koenig 2003), and the vinous breasted starling (in this study) on woodpeckers. In fact, the common myna seems to facilitate the woodpecker breeding, due to its negative interactions with the vinous-breasted starling, which negatively affects the native woodpeckers.

The common myna and the vinous-breasted starling demonstrated different preference for breeding cavities, and although we did not record any nest owner replacement between these two Sturnids, we did record aggressive behavioral interactions among these species around cavities. The two species are partly sympatric in their native ranges (Feare and Craig

1999), overlapping in their breeding timing and in their diet (Feare and Craig 1999). In a nest box experiment in the same study region in the Yarkon Park, Orchan (2007) found that while the nesting boxes in the central, food- and water-rich areas of the park were occupied by the common myna, the vinous-breasted starlings mostly occupied nesting boxes located far from the central, resource rich areas of the park. The vinous-breasted starlings mainly nested closer the periphery of the park, where breeding success was lower.

Vinous-breasted starlings showed strong competition with the native woodpeckers over cavities. Contrary to the mynas, the smaller vinous-breasted starling shares similar cavity preferences with the woodpeckers (Table 2; Fig. 2) and can occupy woodpecker nest without any modification of cavity size and type. They also strongly prefer to nest in intact woodpeckers cavities (Table 3). Indeed, we found that vinous-breasted starlings and woodpeckers interacted aggressively around most of the active woodpecker cavities observed, and we recorded two aggressive nesting woodpecker replacements by the vinous-breasted starling during the woodpeckers' breeding cycle. Thus, these species show contramensalism (\pm). The native Syrian woodpecker, which excavated majority of cavities used for breeding in the park, clearly facilitates the establishment of the vinous-breasted starling. This suggests that the vinous-breasted starlings may pose the largest threat to the native cavity engineers, since they are small enough (Feare and Craig 1999; Cramp and Perrins 1994) to enter the cavity and their nesting period overlaps with the woodpeckers' nesting season.

Even though the native house sparrow is among one of smaller sized species in the cavity-nesting community of the Yarkon Park, it was found to nest in relatively large cavities (Tables 2, 3). The sparrows shared similar nesting preferences with the common mynas and with the parakeets (Fig. 3). No negative interaction was recorded between the native sparrow and woodpecker. However, sparrows and parakeets had more interactions. Sparrows replaced seven pairs of parakeets immediately after the parakeet completed their breeding cycle. In two occasions parakeets replaced the sparrows again before the latter started laying eggs. All sparrow/parakeet replacements occurred either before or after (but not during) completing the nesting cycle. Contrary to the parakeet,

the common myna initiated interactions and replaced sparrows during their breeding cycle, thus reducing their breeding success. The sparrows had the largest bird population of all species in the study region. Most unoccupied nests in the region were first occupied by sparrows, which filled the cavities with nesting material. The sparrows were later replaced by the invasive common myna in many cases or to a lesser extent by the rose-ringed parakeet.

In this study, we did not record direct evidence for interaction of the alien species with two additional cavity-nesting native species found in the area in much lower densities (Shwartz et al. 2008)—the great tit and the scops owl. The fact that we found only one great tit nesting cavity may reflect an impact of the growing population of invasive cavity-nesters in the study area (as may be indicated by the replacement of the cavity-nesting scops owl by the vinous breasted starlings). Point counts that we conducted in the study area between 2003 and 2006 show decline in the great tit population size and increase in abundance of both the house sparrows and the three alien cavity-nesting species (Table 1; Shwartz et al. 2008). This trend may alter the interactions and change the availability of the already limited cavity resource in the region.

Since the Syrian woodpecker population in the study area is relatively small, it is not easy to reliably estimate its population trends. However, one possible future scenario is that the woodpeckers will decline in the region due to the increasing kleptoparasitism (see Kappes and Davis 2008) by alien cavity nesters and that a decline of this important engineer and source for breeding cavities will lead to even stronger competition over cavities, and especially over natural cavities. Kleptoparasitism is defined as a form of competition that involves the ‘stealing’ of already-procured items (Rothschild and Clay 1952; Vollrath 1984). Moreover, enlargement of cavities by the parakeet may negatively affect species that prefer smaller cavities (Remm et al. 2006). This may enable predators (e.g., larger birds, small mammals and reptiles) and competitors such as the mynas to enter the nest more easily (Shwartz et al. 2009). Previous studies have proposed that common mynas can lead to a decline in the breeding success of other bird species (Blanvillain et al. 2003; Currie et al. 2004; Feare and Craig 1999) when they can access the nest. These negative effects found for the common myna can be worse in the case of the smaller sized vinous-breasted starling. The vinous-breasted starling

showed aggressive behavior towards the woodpeckers around cavities and was the only species that replaced the native engineers in their nests during or immediately after the breeding cycle. Thus, the alien vinous-breasted starling can directly and indirectly influence the abundance and richness of other cavity nesters (see Aitken and Martin 2008; Drever et al. 2008 for similar effects among native species).

The results partly support our predictions that the interaction network between different alien species and among alien and native species are shaped by three major factors. These include (a) the nesting preferences of the cavity-nesters (as shown in Table 2 and in Fig. 2); (b) the ability to excavate the cavities (thus increasing the availability of this key limited resource) and (c) the overlap in their timing of breeding. Substantial evidence suggests that cavities are a limited resource in the study area. Of the available cavities, 77 % were occupied during the breeding seasons, representing a high percentage compared with data from more natural environments (Newton 1994; Van Balen et al. 1982; Wesolowski 2007). We recorded successive usage of cavities both within and among breeding seasons, which indicates the potential shortage of this resource (Aitken and Martin 2008). This may imply that the negative interactions between species may well arise from competition over the limited breeding resources and that the woodpecker, the primary excavator, facilitates the secondary cavity nesters by creating or improving the available limited resource—the nesting sites.

Conservation implications and management recommendations

Our results highlight the importance of understanding the interaction web within a community for directing management efforts more effectively. This knowledge may help reduce the undesired outcomes of single species control that may eventually lead to undesired outcomes through changes in interaction pathways (Elmhagen and Rushton 2007; Ritchie and Johnson 2009; Ruscoe et al. 2011). In the nest web studied here, directly managing only one invasive species (population control) may have detrimental effect on other members of the cavity-nesting community. Controlling only the common myna is likely to lead to a competitive release of the vinous-breasted starling, which directly competes with the woodpecker. This

may lead to stronger competition and exclusion of the native woodpecker and may have a counter effect on the management of the community of cavity-nesting birds in the area. On the other hand, control of the rose-ringed parakeet may increase the numbers of the common mynas nesting in parakeet cavities recently enlarged (Table 3; Fig. 2). Our results indicate that the control of the vinous-breasted starling may be the most beneficial management action for the native cavity nesters in the Yarkon Park, as it may lead to competitive release of the woodpeckers from the alien invasive starling and may improve the breeding situation for the native great tits, the house sparrows and for the scops owls.

Another approach is to manage the resources (i.e., the cavities or their size) and by this practice to try and manage the different population consisting the cavity-nesting community. Our results suggest that reducing the size of the large cavities may yield benefits to native species by restricting the larger nesting alien species. This approach may be useful for the smaller cavity nesters such as the great tits, but not for larger species such as the scops owl and woodpeckers. However, it can lead to unexpected spatial effects, for example by driving the invasive parakeets and mynas to disperse from the city to more natural, less managed environments, where their impact on native communities may be worse. It is important to remember that the invasion process in the Yarkon Park is a dynamic and ongoing process in an urban environment and it is therefore not easy to identify its final outcomes.

As can be seen in the relatively simple nest web examined here, with a single engineer and seven major species altogether, the effects of controlling a single alien cavity nester can be complex for the system. Therefore, the interactions between species should be considered in any management program. As woodpeckers can serve as a useful indicator of bird richness and forest health (Drever et al. 2008), monitoring this key species may be a good start for conservation and management programs. Since the Yarkon Park is the source of invasion of most of the alien species in Israel since 1997 (Orchan 2007) and comprises the largest population in Israel for the alien species examined here (Holzapfel et al. 2006; Shwartz et al. 2008; Kark et al., unpublished data), the processes occurring in the park may have important impact on the invasion process in the whole region and has broader applicability to the invasion dynamics of the species involved.

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